Mathematical Demography of the Cape Vulture

Volume 1

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Declaration

I hereby declare that all the research presented in this thesis is my own unaided research unless otherwise acknowledged.

Signed

S.E. Piper

Preface

1) The cut-off date for data-capture, literature, analytical techniques and software packages was 31 December, 1989. No systematic attempt was made to keep up to date during the three years in which the bulk of the text was written.

2) Little field-work or data-collection was undertaken for this research by myself - nearly *ALL* the data come from other workers; they are credited in the acknowledgements.

3) All the data collated for these researches are to be compiled into separate reports to be published by the Vulture Study Group. They can be supplied to interested readers.

4) The work on which this thesis is based has taken me over a third of a lifetime - during which time I have been together many times with Carl Vernon on field trips and with Peter Mundy, John Ledger and Duncan Butchart writing our book *The Vultures of Africa*. During these fifteen years, nearly every topic covered herein has been discussed, sometimes *ad nauseam*, and it is extremely difficult to assign primacy to novel ideas. Where possible, this has been effected by use of the citation 'pers. comm'.

Abstract

The Cape Vulture *Gyps coprotheres* is one of the world's largest avian scavengers and was once widely distributed in southern Africa, to which it is endemic. It has suffered major changes of fortune in recorded history and has, at least twice, undergone large range contractions and expansions in the Cape Province. It has variously been classified as 'rare', 'vulnerable' or 'threatened'. It is currently thought, by some, to be in decline. The central aim of these researches is to answer the 'Grand Question':

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

This is followed by a secondary question:

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

To answer these two questions, all known data pertaining to the Cape Vulture were assembled, analyzed, modelled and synthesized in four *baseline* chapters.

Status and Distribution. (Chapter Three) A total of 441 sites were located at which Cape Vultures bred, roosted, or were suspected of having once done so there. Of these, about 84 are still breeding colonies, and about an equal number are just roosts used for 'over-nighting'. It is estimated that there are 12 000 birds in the population, including 4400 breeding pairs, at these sites. The population is concentrated in two large clusters in a) the Transvaal and Botswana and b) Lesotho, Transkei and Natal. Together they hold over 90% of the population. There are a few other peripheral sub-populations; the most notable are in the Southwestern Cape, Zimbabwe and Namibia. The distribution patterns resulting from the independent data-set derived from bird-watchers, via the Southern African Bird Atlas Project (SABAP), confirm those spatial patterns derived from the site count data. The central nucleus colonies seem to be stable, but many sites on the periphery are declining. The population is in a range-contraction phase.

Fecundity. (Chapter Four) It is shown that the maximum fecundity possible under good conditions in the wild, is likely to be 0.32 female offspring per adult female p.a. Birds start to breed in their fifth or sixth year. There are a number of colonies where this potential is not being met.

Survival. (Chapter Five) Data from the recovery of ringed birds were used to estimate age-specific survival rates, but these estimates were not satisfactory. Much better estimates, for the first two age-classes at least, were made from the resighting of colour-ringed birds in the Southwestern Cape. No adequate estimates of survival are yet available for adults. A number of unnatural causes of mortality were identified as impacting on the population, especially young birds: drowning, electrocution and collision with aerial wires, poisons and direct persecution.

Movements. (Chapter Six) Many young Cape Vultures leave their natal colonies soon after fledging, and wander far and wide across the sub-continent. It is shown that the patterns of the places at which they are found dead has changed dramatically over the last four decades, and it is suggested that this an indication of decreasing population size, range contraction and altered food availability. A model of these movements is presented.

The demographic parameters estimated from the *baseline* chapters were used in a series of mathematical models (Chapter Seven). It was found that the best estimate of adult survival was not consistent with observed population trends and it is suggested that adult survival should be at least 90% p.a. An analysis of detailed demographic data from the Southwestern Cape showed that the adult survival rate could in fact be slightly over 91% p.a. It was also found that fecundity was the critical limiting factor in that sub-population and ways of increasing breeding are suggested. A series of simulation models emphasized the need to obtain a better estimate of adult survival and, if possible, to monitor it in space and time. It is shown that environmental and demographic stochasticity are not serious issues for the two core sub-populations, but are important factors when trying to conserve the peripheral, isolated sub-populations. Permanent movement from the core regions to the periphery, at rates as low as 0.75 individuals p.a., are capable of inhibiting extinction.

From these models a series of recommendations is made (Chapter Eight). Chief among these is the need for an on-going colour-ringing programme to provide uniquely identifiable birds for the purposes of providing better demographic parameter estimates and monitoring. Monitoring of the peripheral sub-populations is as important as monitoring the nucleus breeding colonies.

It is concluded that the Cape Vulture population is secure in its core areas, under current environmental, agricultural and economic conditions, but that the peripheral sub-populations are under pressure and will decline, thereby continuing range contraction. Action is needed to reverse this trend.

Acknowledgements

It is a pleasure to acknowledge and thank all those who have helped me in these researches and in the production of the thesis itself.

For this thesis data have been collected and collated in the following broad categories.

1) Ringed birds. This includes data on ringing, measurements, recoveries, recaptures, resightings, marked birds taken into captivity and dead birds subjected to some form of analysis. Much of this data was collated by Peter and Verity Mundy in the early 1980s. I thank them for sorting out what was an horrendous jigsaw puzzle of a mess. Also thanked are those who supplied the original data and who gave additional data, or helped to get the data-set into some semblance of order. Among them are: André Boshoff (and his staff at the Cape Nature Conservation Division), Christopher Brown, Craig Hilton-Taylor, Joris Komen, Mike Lawes, John Ledger (and his staff at the South African Institute for Medical Research, Vulture Study Group and Endangered Wildlife Trust), Rosalind Lindeque, Peter Mundy, Terry Oatley (and his staff at SAFRING), Alistair Robertson, Dale Schultz, Ann Scott (and her colleagues at De Hoop Nature Reserve), Gerhard Verdoorn (and his colleagues of the Vulture Monitoring Project) and Carl Vernon (and his staff at the National Unit for Bird Ringing Administration and colleagues at the East London Museum). All those members of the Witwatersrand Bird Club and Northern Transvaal Ornithological Society (formerly the Pretoria Bird Club) who kept the ringing records prior to the formation of the Vulture Study Group are also thanked for their efforts and for acting as custodians of these precious data.
2) Check-list data supplied by bird-watchers. The final data-set came to me from SABAP and I gratefully acknowledge James Harrison and his indefatigable team. Also thanked for 'atlas data' are Dale Schultz, Craig Hilton-Taylor, Digby Cyrus, Nigel Robson and the other team members of the 'Natal Atlas'.
3) Breeding data were collected at Colleywobbles by Carl Vernon and are used extensively in Chapter Four. Other breeding data were supplied by Joris Komen and Alistair Robertson. They are thanked.

The general ideas made concrete in this thesis were kicked around many a campfire, seminar white-board, conference room, public bar, kitchen table and university office, over the telephone and via electronic mail with the following: André Boshoff, Christopher Brown, Duncan Butchart, Russel Friedman, Peter Henzi, Craig Hilton-Taylor, Joris Komen, Mike Lawes, John Ledger, Peter Mundy, Dale Schultz, Ann Scott, Gerhard Verdoorn and Carl Vernon. I thank them all for their patience, and hope that I have acknowledged each one of them at the appropriate places in the text for their ideas and suggestions.

In my travels abroad, I have stayed with the following persons, sometimes for part of a day, days or even weeks: Tim Birkhead, Jean Clobert, Martin Gorman, David Houston, Ian Newton and François Sarrazin. Their kind hospitality is acknowledged, as is their interest in the Cape Vulture and its study.

A special word of thanks is due to Ian Newton who made possible a visit to the Institute of Terrestrial Ecology at Monks Wood, Cambridgeshire for the first four months (*'the winter of my content'*) of 1986. Never have I met a more deft practitioner of Occam's Razor. Would that I'd such skill.

Statistical advice was offered by Leslie Underhill, Walter Zucchini, Peter Clarke, John Nelder and Peter Digby - I thank them for their help.

My successive 'bosses' at the University of Natal: Leon Troskie (Mathematical Statistics), Dennis Jenkins and Laurence Eekhout (Surveying and Mapping) and Ronnie Miller (Psychology) are thanked for their tolerance of my fascination with two species of bird, for the goods and services which have been siphoned off for their study, and many hours that I went AWOL on yet another wild vulture (or wagtail) chase. Also thanked are their support staff.

Over 7 500 literature citations were tracked down in the preparation of this thesis (most of them will appear with the supporting documents - not here!) and this would not have been possible were it not for the active day to day support of Debbie Broderick, Felicity Glenn, Dee Neveling and Bonita May Ross. Assistance in tracking down references was also provided by David Kaplan and Dawn Sholto-Douglas. Finding literature in specialist libraries was made easier through the kind offices of many people. The two institutions most used were the Niven Library at the University of Cape Town (Richard Brooke, John Cooper and their staff) and the Alexander Library at the Edward Grey Institute, Oxford (Chris Perrins and especially Linda Birch). Other libraries used were those at the Universities of Natal (Durban and Pietermaritzburg), Cape Town, Cambridge and the Natural Science Museum Library in Durban (Belinda Eisenhauer). David Houston, Russel Friedman, Peter Mundy and Philip North (dispersal bibliography) made useful material available to me. All are thanked. All this material was put onto a bibliographic database, called GLitch, and written for me by Dale Schultz. It would not have been possible to keep track of all this material were it not for GLitch and Dale's much appreciated efforts.

The Director and staff of the University of Natal's Computer Service's Division are thanked for their assistance and access to their equipment.

Pam Holy is thanked for her sterling data-capture efforts.

Three sections of these researches are the results of collaboration with colleagues:

1) The literature review of Chapter Two is drawn from the reviews in Chapters One to Four, and the Cape Griffon species' account of Chapter Five, of our book *The Vultures of Africa*[1].
2) Ms. Lindsay McNeill of the Department of Statistical Sciences at the University of Cape developed the binomial-kriging-generalized linear model used for spatial interpolation of the reporting rate used for the SABAP data of section 3.2.5.
3) Carl Vernon was the driving force behind the collection and analysis of the Colleywobbles breeding data of Chapter Four.

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[1] Mundy, P.J., Butchart, D, Ledger, J.A. and Piper, S.E. 1992. *The vultures of Africa*. Acorn Books & Russel Friedman Books: Johannesburg.

'How the Camel got his Hump' from 'The Just So Stories' by Rudyard Kipling (1902)
Macmillan: London.

no sooner had he said it than he saw his back, that he was so proud of, puffing up and puffing up into a great big lolloping humph.

'Do you see that?' said the Djinn. 'That's your very own humph that you've brought upon your very own self by not working. To-day is Thursday, and you've done no work since Monday, when the work began. Now you are going to work.'

'How can I,' said the Camel, 'with this humph on my back?'

'That's made a-purpose,' said the Djinn, 'all because you missed those three days. You will be able to work now for three days without eating, because you can live on your humph; and don't you ever say I never did anything for you. Come out of the Desert and go to the Three, and behave. Humph yourself!'

And the Camel humphed himself, humph and all, and went away to join the Three. And from that day to this the Camel always wears a humph (we call it 'hump' now, not to hurt his feelings); but he has never yet caught up with the three days that he missed at the beginning of the world, and he has never yet learned how to behave.

THE Camel's hump is an ugly lump
Which well you may see at the Zoo;
But uglier yet is the hump we get
From having too little to do.

Kiddies and grown-ups too-oo-oo,
If we haven't enough to do-oo-oo,
We get the hump—
Cameelious hump—
The hump that is black and blue!

We climb out of bed with a frouzly head
And a snarly-yarly voice.
We shiver and scowl and we grunt and we growl
At our bath and our boots and our toys;

And there ought to be a corner for me
(And I know there is one for you)
When we get the hump—
Cameelious hump—
The hump that is black and blue!

The cure for this ill is not to sit still,
Or frowst with a book by the fire;
But to take a large hoe and a shovel also,
And dig till you gently perspire;

And then you will find that the sun and the wind,
And the Djinn of the Garden too,
Have lifted the hump—
The horrible hump—
The hump that is black and blue!

I get it as well as you-oo-oo—
If I haven't enough to do-oo-oo!
We all get hump—
Cameelious hump—
Kiddies and grown-ups too!

Computer suites were written for me by Dale Schultz (GLitch - bibliography), Patrick Matibe (SAMap - map projection transformations), Simon Bernstein (IRP - image conversion) and Aviad Eyal (VULTURE - site register).

Useful comments on individual chapters of were supplied by James Harrison, Peter Henzi, Leslie Underhill and Carl Vernon.

The Dean of Science, University of Cape Town, Prof. V.C. Moran and acting Dean, Prof. G.M. Brundrit are both thanked for wielding the 'big stick', but not too viciously!

The thesis was read in its entirety by my two supervisors Doug Butterworth and Peter Mundy. I thank them both for battling valiantly with my turgid prose and obtuse style. I also thank them for their efforts, patience, guidance and encouragement.

Financial support was provided for various thesis- and vulture-related activities by the Vulture Study Group, Endangered Wildlife Trust, University of Natal Research Committee, Natal Bird Club and Southern African Ornithological Society. They all thanked.

The final responsibility for this work is my own; by thanking the above I do not imply that they agree with my interpretations of the data, choice of analytical techniques or interpretation of the results.

My association with the Vulture Study Group has been a great source of inspiration and comfort to me - I have enjoyed that special warmth that comes from friendships based on a common interest - I thank all those 'vulcha luvas' who have enriched my life and appreciate the way they have tolerated my passion for this bizarre hobby.

To my dear wife, Andy, my thanks for creating '*The peculiar conditions necessary for writing - some measure of solitude, a contemplative atmosphere* ...'[2]. She, and our children (now happily fledged) seemed to have remained sane and normal and unaffected by this, my *Camelus* hump.

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[2] Ruth Rendell, 1985 p.16. The tree of hands. Arrow Books: London.

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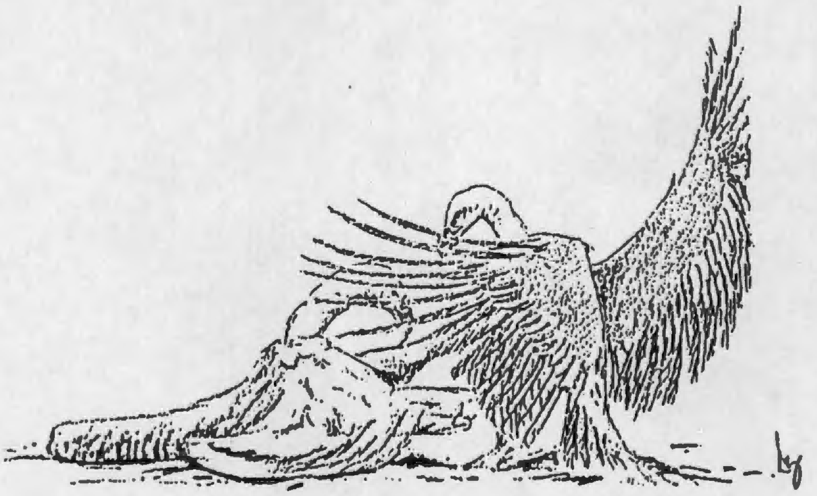
List of Figures

All the sketches in the thesis come from the book *The vultures of Africa* and were drawn by Duncan Butchart. I am grateful to him for permission to reproduce them. I am only sorry that his fine and delicate line drawings do not reproduce well when photocopied.



Chapter One

Introduction

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Chapter One

Introduction

On a warm autumn afternoon it is possible to stand on the hilltop above Colleywobbles and watch upwards of a hundred Cape Vultures silently soaring up and around in a *circus* with pairs, triplets and even groups of four, five and six birds trying to tandem, one with another. It is a wondrous sight, all that seemingly effortless movement, both graceful and acrobatic. Since first watching this magnificent airborne scavenger at Colleywobbles, some 16 years ago, I have been fascinated by this bird and its ability to survive in our modern environment, so changed by human action.

This introduction first describes the reasons for choosing the Cape Vulture as a study species, the need for integrated management and rôle of modelling. The research objectives are then summarized. The data-sets used in this study, and their sources are outlined. In modelling populations it is possible to take a number of different approaches: those chosen here are motivated. To provide coherence and consistency, the statistical and bibliographic conventions used are listed. A brief description is given of the computer software packages employed.

1.1 Reasons for choosing the Cape Vulture

In my opinion all birds are interesting. You just have to ask the right questions.

So why the Cape Vulture? Given that all birds are interesting, it is possible to fetch up, *post hoc*, apposite reasons for studying any particular species. Thus it is important to admit that the primary motivating force for this writer is one of personal prejudice, or inclination. After that, supposedly rational reasons can be motivated. Reasons for protecting species (and probably for studying them) generally fall into one of five categories: ethical, aesthetic, economic, scientific and ecological (Halliday 1978); these reasons have been discussed in the context of southern Africa and its Third World environment (Siegfried 1984: 119 ff.).

The reasons advanced for choosing the Cape Vulture as the subject of an exercise in demographic modelling are explained below.

1) The Cape Vulture is for many people an *indicator species*, but it is probably not a *keystone species*. A keystone species is 'one that, by its effective disappearance from a system, results (directly or indirectly) in the virtual disappearance of several other species' (Soulé & Kohm 1989: 23). It has been argued (Siegfried 1984: 122) that southern African vultures have:

> evolved as "consequences" rather than "determinants" of certain ecological processes, and their roles as "reducers" in ecosystem functioning can be filled by substitutes.

It is probably true that the Cape Vulture is not a keystone species. The Cape Vulture is a scavenger at the top of the pyramid and is itself not prey for any other species, except for an array of parasites (at least one of them specific to the Cape Vulture: the tick *Argas zumpti*: Mundy, Butchart, Ledger & Piper 1992: 319, 431). As a scavenger, it once competed with mammalian scavengers (e.g. Lion & hyena) but no longer does so - thus its demise will not influence any other large scavenger. The only possibility is that with its disappearance, the number of carcass-disposing flies will increase and there will be a concomitant rise in fly-borne diseases. On the other hand, *indicator species* are selected because 'their population changes are believed to indicate the effects of management activities ... and because they represent a particular use, ecosystem, or management concern. They are not necessarily keystone species' (Soulé & Kohm 1989: 25). Over the last fifteen years the Cape Vulture has become the symbol of conservation outside the formal game reserve areas of southern Africa. It is my *opinion* that the conservation of the Cape Vulture will lead to the preservation (or at least a slower degradation) of much of the savanna ecosystem in the subcontinent.

2) Given that a vulture species is to be studied in southern Africa then it is certain that the Cape Vulture is the bird with the highest 'public profile' as judged by news reports and comment in the public communications media (*pers. obs.* based on the collection of press cuttings maintained at the Endangered Wildlife Trust in Johannesburg). Thus, in my *opinion*, any research on the species will be well-received by the community at large.

3) The Cape Vulture can still be found in fairly large numbers throughout the eastern portion of southern Africa. It also occurs largely outside formal conservation areas. Thus it is easy to see it, and study it, at its roosts and colonies without the delay of

having to go through the bureaucratic channels of the nature conservancies. Because of the species' wide geographical distribution it is possible, in my *opinion*, to design protection, monitoring and management schemes which can be undertaken effectively by volunteer and non-government organizations.

4) Because of its abundance and large size the Cape Vulture has attracted much attention. There is a considerable body of literature on this species and the basic biology is fairly well known. It has been the subject of a number of postgraduate research degrees (see summary in Mundy, Butchart, Ledger & Piper 1992: 400-402).
5) Considerable effort has been devoted to marking Cape Vultures and monitoring their subsequent fate, both in space and time (see below).

1.2 Integrated management and the rôle of modelling

Since the early 1980s the conservation philosophy of the Vulture Study Group has been based on a seven-point 'Integrated Management' plan (Plunkett 1978).

1) Research.
2) Protection.
3) Education.
4) Management.
5) Population modelling.
6) Population monitoring.
7) Coordinated overall planning.

The way in which this plan was put into action, and its successes, failures and appropriateness, have been described elsewhere (Mundy, Butchart, Ledger & Piper 1992: 400-402). Considerable effort has been devoted to research, protection and education by a number of Universities, members of the Vulture Study Group and the Vulture Monitoring Project. Given the funds available, the results must be judged both successful and cost-effective. Less effort has been expended on management, population monitoring and coordinated overall planning where the results have been less spectacular (loc. cit.)

A strong motivation for the research on which this thesis is based came from the Vulture Study Group's desire to have a population modelling exercise undertaken for each vulture species. This thesis is in response to that desire, and ends (see Chapter Eight below) with a set of recommendations for population monitoring.

1.3 Research objectives and questions

The general objective of constructing a 'population model' is too broad and diffuse to act as the guiding light for a single piece of research, such as this. To provide a tighter focus, a single 'Grand Question' is asked.

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

This is followed by a secondary question.

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

To use a model, or series of models, to answer these questions it is necessary to have some idea of the values of the demographic parameters and variables. Unfortunately few estimates are available, and such as have been made are of poor quality. Thus it is necessary to provide estimates of the values of the demographic parameters and variables. To this end, four distinct data-sets are collated and investigated in four *baseline* chapters, each of which has its own specific objectives or research questions. These are now described.

Chapter Three. *Status and Distribution.*

1) How many Cape Vultures are there, and what is the age and sex composition of the population?
2) What is the spatial extent, or distribution, of the population?
3) Are there any regions in which the population is currently increasing or decreasing sharply?

Chapter Four. *Fecundity.*

1) How many live young can a pair of Cape Vultures produce each year?
2) How does fecundity vary through the population in space and time?

Chapter Five. *Survival.*

1) What is the annual survival rate of each age-class?
2) What natural and unnatural mortality factors act on the population?

Chapter Six. *Movements.*

1) How do Cape Vultures distribute themselves in space from the time they leave their natal colonies to about five or six years later (if they survive that long), when they are recruited into the breeding segment of the population?
2) What evidence is there for philopatry and natal fidelity?

Using the insights and estimates of demographic parameters and variables provided by the four *baseline* chapters, a series of models will then be built in Chapter Seven with the aim of answering the 'Grand Question' posed above.

In April 1983, an open meeting was held in Johannesburg, after the 'Birds and Man' symposium, at which it was decided to stop ringing Cape Vultures and to bring together all the data that had been gathered on them so as to provide an overall assessment of the species' status with recommendations for future data-collection, monitoring and research. This thesis, with its supporting documents is one response to that decision.

1.4 Available data-sets

The estimates of the demographic parameters and variables used in this thesis are based on the analyses of four large data-sets (and a bibliography) which were collated specifically for the purpose of modelling the Cape Vulture population. They are described in order of use.

Site Register. There are about 440 sites in southern Africa which are breeding colonies, or roosts, or are suspected of once having been so. Each site is documented in a draft report entitled - *Site register of the Cape Vulture: Ancient and modern.* It currently runs to about 300 pages and is authored by S.E. Piper, P.J. Mundy and C.J. Vernon. The documentation of each site covers geographic, physiographic and bioclimatic features, land tenure, land use patterns, an assessment of the demographic and conservation status as well as a complete record of every known visit to the site and resultant observations. A full bibliography of all published and unpublished material, where known to the authors, is appended to each site's register sheet.

SABAP. The Southern African Bird Atlas Project, based in the Avian Demography Unit of the University of Cape Town's Department of Statistical Sciences, has collated all known species check-lists compiled by bird-watchers in southern Africa. These data are organized into grid-cells of dimension ¼° latitude by ¼° longitude for each calendar month of the year. For this thesis, I purchased the entire Cape Vulture data-set for South Africa (as per the 1960 Union boundaries - which included all the so-called 'independent homelands'), Swaziland and Lesotho. This data-set is used to map the spatial distribution of the species by means of the reporting rate (i.e. the proportion of check-lists reporting Cape Vultures).

Colleywobbles breeding data. For the decade of the 1980s, a record was kept of the breeding activity at every nest on "Main Face" at the Colleywobbles Cape Vulture breeding colony. These data have already been published (Vernon & Piper 1991). They are to be used to estimate the proportion of adults which breed in any given year, as well as the breeding success and its variations from year to year.

Marked birds. The first Cape Vulture was ringed in the Transvaal in 1948. Since then over 7000 have been ringed using a metal ring, while over 3000 of these were also fitted with a set of colour-rings. Many of these birds were measured when ringed (e.g. wing length and mass). Some have subsequently been recaptured, resighted or recovered. Some were taken into captivity or killed for experimental purposes. All the data relating to these birds are gathered together in a draft report - *Marked Cape Vultures: all birds handled to 1990.* This report runs to about 300 pages and is authored by S.E. Piper, P.J. Mundy and V.S. Mundy. These data will be used to estimate age-specific survival rates, for an investigation of the effects of unnatural causes of mortality and the study of movements.

GLitch. There is an extensive literature on the Cape Vulture, much of it anecdotal and trivial, spread across a wide range of publications. All issues of the following journals and magazines were searched: *Bokmakierie* (now *S.A. Birding*), *Honeyguide*, *Ibis*, *Ostrich* and *Vulture News*, because they hold most of the more 'scientific' reports. Each paper was photocopied and all its citations traced. Then a complete search was undertaken of all the 'grey' literature in southern Africa (mainly the 18 bird club news-sheets; see list in Ledger 1987) by the laborious process of scanning every page of every issue. All material located was placed on a computerized bibliographic data-base called GLitch (Global Literature search) with an abstract, source (i.e. holding library where located) and a liberal assortment of keywords. A total of 997 references to the Cape Vulture has so far been located and catalogued and will be issued later as a Vulture Study Group report.

1.5 Modelling philosophy

> A model is any representation or abstraction of a system or a process. We build models because they help us to (1) define our problems, (2) organize out thoughts, (3) understand our data, (4) communicate and test that understanding, and (5) make predictions. A model is therefore an intellectual tool (Starfield & Bleloch 1991: 1).

A clear and succinct description of the variety of philosophical approaches to modelling has been provided by Holling (1978), and expanded upon by Starfield & Bleloch (1991: 2-3). Their classification is best portrayed graphically (Figure 1.1). The four 'compartments' are described as is their applicability to these researches.

A) Good data, but little understanding of the problem. This situation is amenable to the highest level of exploratory statistical analysis (e.g. Tukey 1977), followed by the construction of appropriate statistical models.

B) Poor data, but some understanding of the problem. This combination often arises in biology because a similar species has been studied. If that species has a similar 'lifestyle' then the structure of the model may be obvious, but the values of the parameters will be poorly known. Analogues for the Cape Vulture will be other griffons, other vultures, or even marine scavengers (e.g. Skuas, Giant Petrels).

C) Good data and good understanding. It will be seen that the breeding data at Colleywobbles come closest to this.

D) Poor data and little understanding of the problem. Regrettably, in my opinion, most biological modelling languishes in this "loser's corner of the boxing ring".

The position of the modeller has been summarized (Starfield & Bleloch 1991: 3) in the following manner.

> We therefore build models to *explore the consequences* of what we believe to be true ... Because we have so little data in areas B and D, we learn by living with our models, by exercising them, manipulating them, questioning their relevance, and comparing their behaviour with what we know (or think we know) about the real world ... The process is one of *boot-strapping*: If we begin with little data and understanding in the bottom left-hand corner of Holling's diagram, models help us to zigzag upwards to the right .

Classification of Modelling Problems

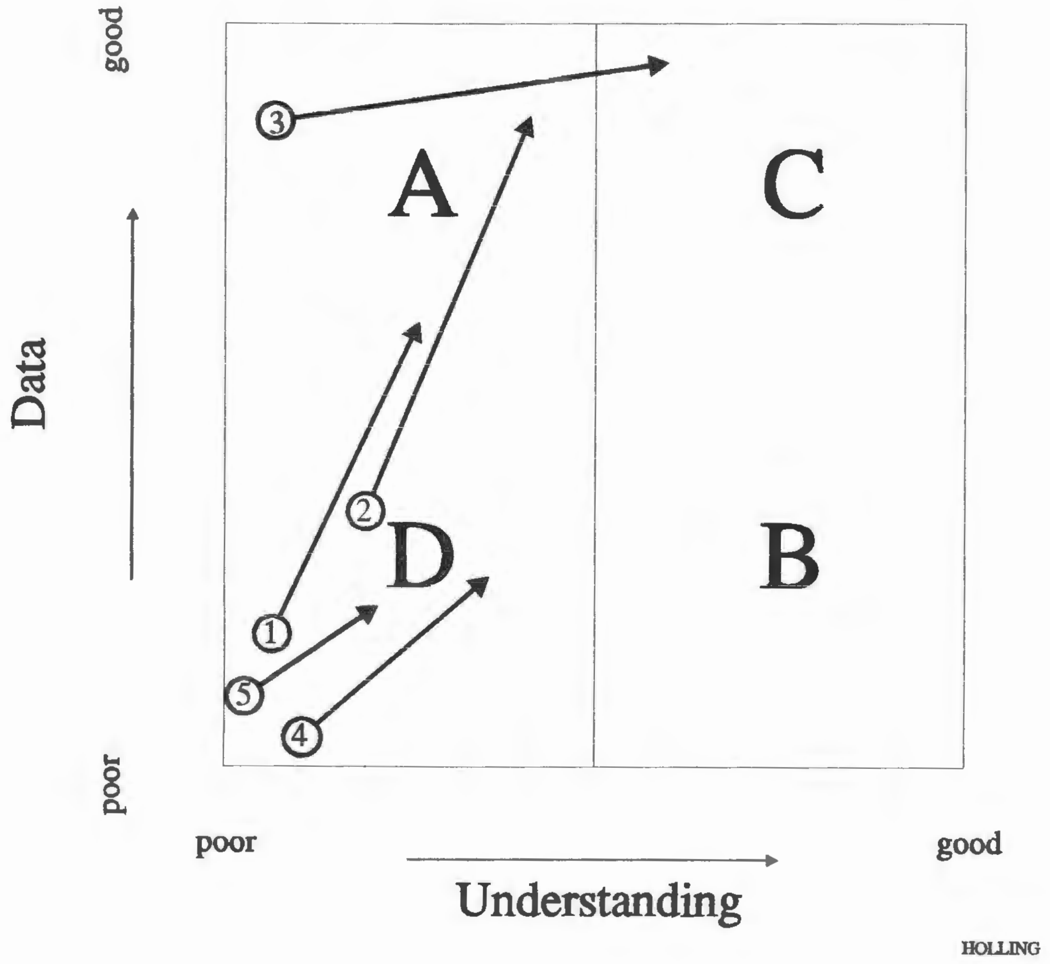


Figure 1.1. Classification of modelling problems, modified from Starfield & Bleloch (1991) and based on Holling (1978). Vectors represent the relative improvement of data and of understanding of the following demographic parameters analyzed in these researches: 1 = Status, 2 = Distribution, 3 = Fecundity, 4 = Survival and 5 = Movement.

I feel it important to state, 'up front' (as they say in North America), that I am personally disinclined to build models in advance of the data. Without supporting data, there is no way of knowing if the conclusions drawn from the model are relevant to the conservation of the species under study. However, as has been pointed out:

> Those who collect data without building models run the very real risk of discovering, when they eventually analyze their data, that they have collected the wrong data! (Starfield & Bleloch 1991: 3)

The analyses of each of the data-sets for the purposes of estimating demographic parameters is assessed in terms of the quality of the data and the extent of the understanding of the underlying models, both when the analysis was begun and when it ended (Figure 1.1).

1) *Status.* Little data were to hand before the start of these researches and knowledge of the Cape Vulture's population size and extent was poor. The data presented in Chapter Three give a good idea of population size and structure, but an inadequate picture of changes over time.
2) *Distribution.* Most distribution maps of the Cape Vulture are wrong and too optimistic, showing occurrence even where there has never been a sight record. The SABAP data-set gives an excellent picture of the current distribution.
3) *Fecundity.* This is the best-known area of Cape Vulture demography. With the data from Colleywobbles, there are now excellent estimates of breeding success. Estimates of the proportion breeding are not as good, and there is only a poor understanding of how productivity varies across the sub-continent.
4) *Survival.* The quantity and quality of the data, of understanding of survival and of the estimates of age-specific survival rates, are extremely poor. As a result of the data collated and analyzed herein, this situation has improved.
5) *Movements.* Other than for a few anecdotal accounts and speculations concerning movements, philopatry and natal-site fidelity, almost nothing was known of these topics. The data collated, summarized and mapped herein have increased understanding of the basic movement processes, but more observations of specific spatial processes are required.

In each Chapter, cognizance will be taken of the literature on the modelling and statistical analysis philosophies appropriate to the demographic parameters and variables under consideration (e.g. Clobert & Lebreton 1991: 76 for fecundity estimates).

1.6 Statistical and bibliographic conventions

An attempt has been made to adhere to the following conventions throughout the thesis.

Statistical

Significance.	A result is deemed to be 'significant', in the sense of statistical significance, if the probability of a type I error is less than 5%.
Goodness-of-fit.	The goodness-of-fit, when applied to count-data, is measured by using the Chi-squared test and accepted as 'good' if $p > 5\%$. Note that in the case of fitting generalized linear models (GLM) the deviance of the residuals is used, although it is only asymptotically distributed as chi-squared.
Linear Regression.	The overall quality of linear regression is measured using the F-ratio at the 5% level of significance.
Under- or over-estimated vs biased.	Unless the true value of a parameter is known, it is generally not possible to say if an estimator is over- or under-estimating the true value. The best one can say is that the estimate is positively or negatively biased.

Bibliographic

All references are handled in the way usual for scientific journals and theses, except for the following small differences.

Citations.	All citations in the text are given in full, e.g. (Mundy, Butchart, Ledger & Piper 1992), not (Mundy *et al.* 1992). In this day and age of computers and word processors, this is no extra trouble and makes automated searching for citations easier.
Reference list.	All authors are stored with their full set of initials and the correct spelling of their names. Bibliographic data-bases store the following names in separate sequences: /Ledger, J./Ledger, John/Ledger, J.A./. Given that the compiler knows that the author was /Ledger, J.A./ there is no logical or sensible reason why it should not be recorded as such. I am hugely irritated by the use of *[sic]* and refuse to catalogue /Ledger, J.A./ under /Ledjer*[sic]*, J.A./, even if the author's name was misspelt

	in the original paper . There is no logical reason for perpetuating the errors of the past - especially when this totally confuses the computerized bibliography.
Journal names.	Given in full, if known. There are so many obscure journals that it is helpful to the reader to have the name in full - especially in a thesis such as this where discipline boundaries are crossed.
Series, number and page numbers.	The series and issue numbers are given, if known. The page numbers are given in full, if known.

These changes are designed to make life a little easier for the reader. Once this detail is on the computer it stays on, and stays on correctly.

1.7 Software packages

In 1986 a decision was made not to write computer programs; instead computer packages would be used - if the appropriate one did not exist then the problem was not soluble! The packages listed below were used. A brief description of each is given, as well as an indication of where it was used. Only software legally acquired was used.

Clipper.	A dBASE-like program which produces compiled 'executables' that can be run on any DOS system. Used to write the 'GLitch' and 'VULTURE' suites described below.
Corel Draw! 2.1 & 3.0.	A general-purpose drawing and illustration package used for many of the figures.
dBASE III+.	The data-base package used for nearly all data-capture, manipulation, sorting, indexing, retrieving and report writing.
dBXL.	A dBASE clone, sometimes used as an alternative to dBASE.
Dragon Level 2.	An image processing suite used to produce and enhance some of the figures.
GENSTAT 5 1.3.	A high-level statistical package used for all the generalized linear models (GLM) and some other statistical analyses.

GLitch.	A computerized bibliographic package written specifically for this thesis by Dale Schultz (Computer Services, University of Natal, Durban) programming in Clipper.
IDRISI.	An image processing and geographic information systems (GIS) package used to enhance and produce some of the figures.
Binomial Kriging package.	Written and used by Lindsay McNeill (Statistical Sciences, University of Cape Town) for interpolating Cape Vulture reporting rates.
MapBox 1.6.	A GIS package used for some of the spatial interpolations.
Mathcad 3.0 & 3.1.	A general-purpose mathematical 'sketch-pad' used for model-building and evaluating a variety of mathematical functions. It comes with a subset of the Maple Symbolic Processor and is used for symbolic processing of a variety of problems in algebra, integration and differentiation. The 'Circular Statistics' module of Chapter Six was written in Mathcad.
Quatro Pro.	A spreadsheet package sometimes used instead of VP Planner+ (see below).
RAMAS/age.	A simulation package used to model age-structured populations.
RAMAS/space.	A simulation package used for meta-population analysis.
SAMap.	This package was written for me by Patrick Matibe (Surveying and Mapping, University of Natal, Durban), in FORTRAN, to convert coordinates from one map-projection to another, via geographical coordinates.
Semper 6P.	A powerful image processing toolkit used for producing some of the images and figures.
STATGRAPHICS 4 & 5.	The workhorse for nearly all the routine computations, statistical analyses and graphical output.
Surfer.	A contouring package extensively used herein, and also used as a mapping package.
VP Planner+.	A Lotus 1-2-3 clone used for spreadsheets and many once-off and what-if calculations. Now superseded by Quatro Pro and sued to extinction by the Lotus Corporation.

VULTURE.	A special purpose package written for me by Aviad Eyal (Computer Sciences, University of Natal, Durban), in Clipper, to keep track of the Site Register data.
XyWrite 3.5.	The trusty ol' word-processor!

Utilities from a number of sources were used: Chop (to transport large files), Clip Art, DOS, IRP (image reformatting package), Lotus Magellan (circumnavigates your hard drive - finds all those things you lost in obscure files), Norton Utilities, PC Tools, SEII (hand-held scanner), Tapeout and WINDOWS 3.0 and 3.1

1.8 Thesis structure

The biology of vultures in general, and of the Cape Vulture in particular, is described in Chapter Two. The numerical status, spatial distribution and temporal changes are investigated in Chapter Three. In Chapter Four an estimate of fecundity is provided. The process by which ringed birds are recovered (i.e. found dead and reported) is investigated in Chapter Five. Techniques of estimating survival from recoveries and from resightings are also described. A variety of topics connected with movements is discussed in Chapter Six.

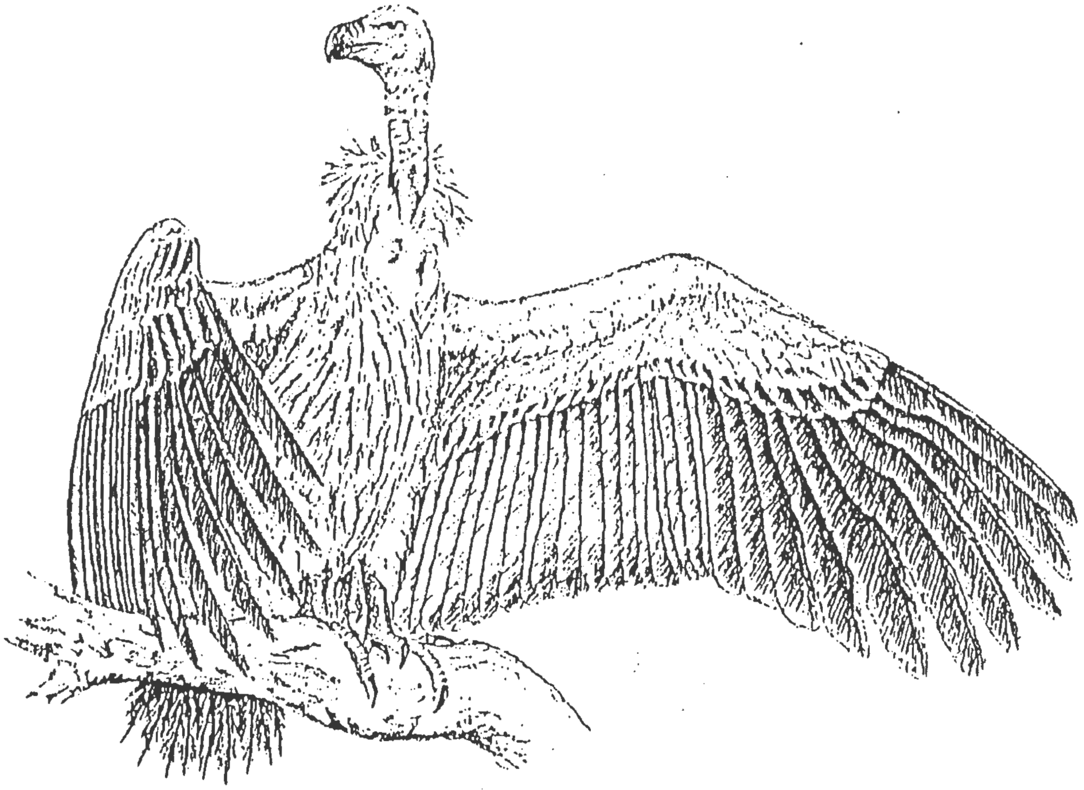
Models of Cape Vulture populations are built in Chapter Seven. Consideration is also given to environmental and demographic stochasticity. A meta-population analysis is also performed. The effects of permanent movements between spatially disjoint sub-populations are simulated with a view to the estimation of extinction probabilities.

In the last chapter (Eight) the results of the analyses are discussed, conclusions are drawn and a set of recommendations for future research, conservation and monitoring are presented.

Chapter Two

Biology of the Cape Vulture

Contents



Chapter Two

Biology of the Cape Vulture

Useful, accurate and appropriate demographic models are likely to be based on a good understanding of the species' biology, especially as it relates to its 'life history'. Nevertheless, there will be many aspects of a species' biology which will not impact on the species' population dynamics, except in the most peripheral way. Thus the demographer is generally not interested in details of physiology, ethology and anatomy.

The characteristics of vultures, in general, will first be described and this will be followed by a short summary of vulture taxonomy. Against this backdrop, a picture will be painted of the Cape Vulture, with special emphasis on those aspects of its biology relevant to estimating demographic parameters.

The whole 'vulture world' has been reviewed in general, and African vultures in particular, in a recent book (Mundy, Butchart, Ledger & Piper 1992: *The vultures of Africa*) and this chapter will be drawn largely from that work. At the start of each section an indication will be given, via a footnote, of the portion of the book from which the review is drawn. The theoretical framework of raptor ecology is drawn from Newton (1979, 1989, 1991).

2.1 What is a vulture?[1]

There are currently 22 species of vulture, 15 of these are be found in the Old World and seven in the New World. Although they look alike (anyone can recognize a vulture), it is now known that these two groups are quite distinct and have no genetic relationship, i.e. they have no common ancestor - at least not in the last 20 million years.

Vultures are avian scavengers having evolved from at least two different roots (see section 2.2 below). The features they share are a near-bald head, large body-size, flat feet, hooked bill, and they feed on carcasses, are often seen in congregations on the ground, and they soar wonderfully well, which is part of their foraging technique. There are other birds which come close to this loose specification, e.g. Marabou Stork *Leptoptilos crumeniferus* but argument will be avoided by confining attention to the 15 Old-World vultures (Figure 2.1).

Form and function are intertwined and so will be discussed together.

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[1] See Chapter Two in Mundy, Butchart, Ledger & Piper (1992).

1) *Physical characteristics.* Each feature will be described along with its probable function.

A) Near-bald head and neck. This is an obvious adaptation to the messy nature of a carrion-feeding way of life. The degree of baldness and down-cover varies among species. The colour of the bare skin and the degree of downy-cover may serve other functions, including thermoregulation and communication.

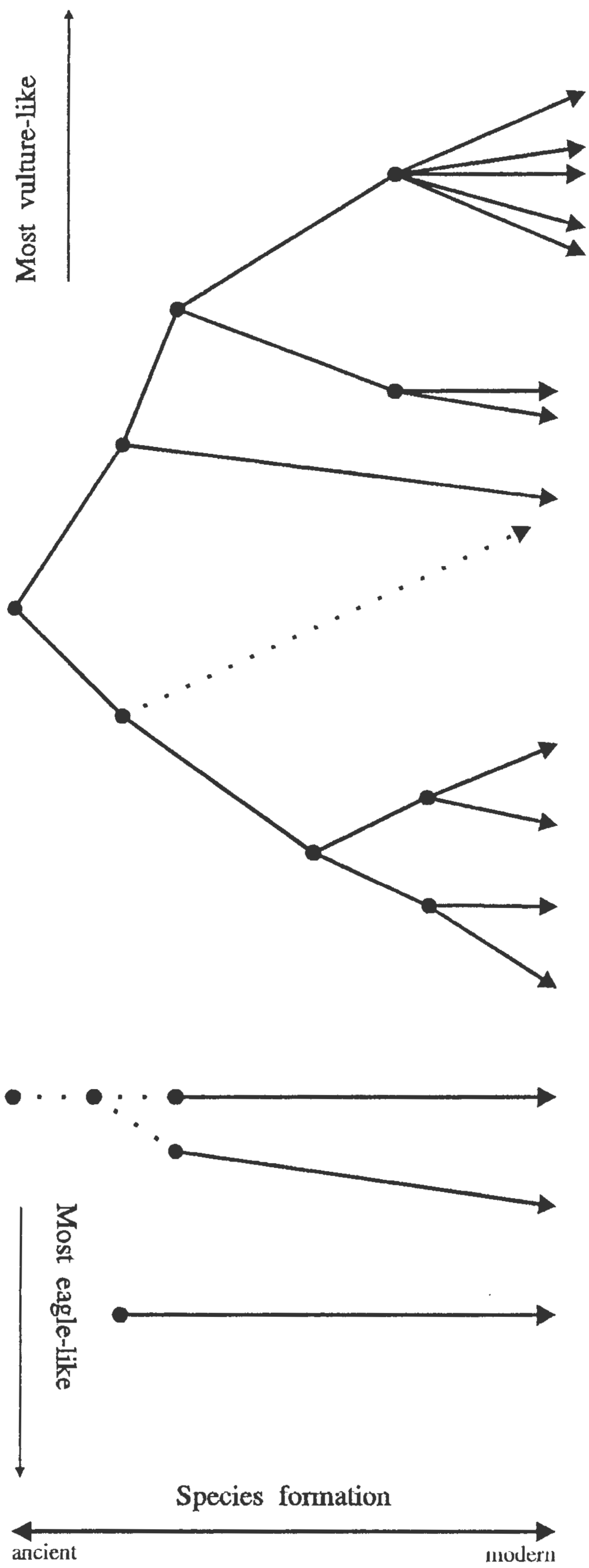
B) Hooked bill. All vultures have a hooked bill, the most powerful being found on the Lappetfaced Vulture which uses it for tearing skin and tendons and for killing. The *Gyps* and *Pseudogyps* species feed rapidly in competition with each other, often ‘skinning’ a carcass from the inside taking muscle, viscera and fat and swallowing it rapidly, aided by their large tongues (which have well developed tongue-bones in them). A Cape Vulture can swallow up to 1.5 kg in some 2 - 5 minutes.

C) Eyesight. Some vulture species have had their visual acuity measured. This has been rated at twice that of humans, certainly not greater as suggested by folklore. Most griffons form a foraging-net while feeding, and it is likely that this combined searching yields better food-finding results. If this is so, then it may be that below a certain local population size (or density) they may not be able to forage effectively. None of the Old-World vultures has any appreciable sense of smell and so they rely entirely on their eyesight to find food.

D) Crop. All vultures have a crop which acts as a temporary ‘shopping bag’. In the Cape Vulture the crop can hold up to 1.5 kg, which is about 16 to 20% of the adult mass and is an adaptation to the species’ feast-and-famine lifestyle. Food is unpredictable in space and time, but the ‘parcel size’ is much greater than any one bird can eat. The larger vultures can fast for up to two weeks, perhaps more, lose one third of their body mass and still survive.

E) Size. Vultures are all large birds, some have a body mass of over 8 kg.

F) Sexual dimorphism. In only one species of Old-World vulture (Whiteheaded Vulture) is there any marked difference between males and females, in terms of size (the female is larger) and plumage. However, in most species there is a slight size dimorphism within a breeding pair, with the female larger than the male. In general terms, species without sexual size dimorphism tend to have both males and females performing similar rôles in terms of their life history and this means they can, as a first approximation, be treated identically in demographic models.



Latin binominal	Common name
Gyps	Griffons
coprotheres	Cape
fulvus	Eurasian
indicus	Longbilled
himalayensis	Himalayan
rueppellii	Rüppell's
Pseudogyps	Whitebacked Vultures
africanus	African
bengalensis	Indian
Necrosyrtes *monachus*	Hooded Vulture
Aegypius *monachus*	Cinereous Vulture
Torgos *tracheliotos*	Lappetfaced Vulture
Sarcogyps *calvus*	Pondicherry Vulture
Trigonoceps *occipitalis*	Whiteheaded Vulture
Neophron *percnopterus*	Egyptian Vulture
Gypaetus *barbatus*	Bearded Vulture
Gypohierax *angolensis*	Palmnut Vulture

Figure 2.1 Taxonomy of Old-World vultures.

2) *Flight.* All vultures are good fliers; some are even migrants. The larger vultures are constrained by their size and physiology to be gliders and soarers; sustained flapping flight is not possible for more than a short while for the griffons. Gliding is carried out in still air, while soaring occurs in an upwardly moving air column. Vultures use both, and the large griffons are able, in environments with good, regular and predictable thermals, to fly regularly up to 150 km per day away from their colony to feed, and then return again. This puts a limit on the 'activity zone' of those birds tied to a colony.

3) *Inter- and intraspecific aggression.* There is much fighting among all sorts of birds. Fighting is almost a daily event. Fighting occurs among members of a species and also occurs between species. All this conflict and physical combat must surely lead to damage and occasional impairment. In turn impairment may lead to starvation and death.

2.2 Vulture taxonomy[2]

The taxonomy of vultures is in a state of flux because raptor taxonomy is unsettled. In the broadest terms, vultures can be divided into a group of seven New-World vultures and 15 Old-World vultures. The New-World vultures are not raptors, but are probably derived from one of the water-bird groups; some would suggest that they are modified storks.

The 15 vultures found in the Old-World are all raptor-like, but are not derived from the same root-stock (Figure 2.2.A). It is probable that 12 of them have a common ancestor, the so-called 'aegypiins' comprising the four 'dark' vultures: *Aegypius*, *Torgos*, *Sarcogyps* and *Trigonoceps*; the five *Gyps* species (i.e. griffons); the two *Psuedogyps* species (i.e. Whitebacked vultures); and *Necrosyrtes* (Hooded Vulture). The remaining three vultures come from different roots, though there is a slight possibility that *Neophron* and *Gypaetus* vultures share a common ancestor.

2.3 Status and distribution[3]

The Cape Vulture is currently confined to an area of about $3.5 \cdot 10^6$ km^2, entirely to the south of 12°S, but once could be seen in Namibia, Botswana, Mozambique (south of the Zambezi River), much of South Africa (as per the Union of South Africa borders in 1960), Swaziland and Lesotho. There are occasional sightings north of this region in Zambia (confirmed), as well as one record from Zaïre (doubtful).

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[2] See Mundy, Butchart, Ledger & Piper (1992 p. 27-28).

[3] See Mundy, Butchart, Ledger & Piper (1992 p. 76-79; 96-99).

Table 2.1
Summary of Cape Vulture population estimates

Region	King (1981) birds	King (1981) pairs	Collar & Stuart (1985) birds	Collar & Stuart (1985) pairs	Brooke (1984a) pairs	Brooke (1984b) pairs
Botswana	-	-	-	300	?	?
Cape	-	-	-	100	65	100
Lesotho	-	-	-	250	90	200
Mozambique	-	-	-	Ca.200	?	?
Namibia	-	-	-	50	?	?
Natal	-	-	-	200	37	200
OFS	-	-	-	?	18	50
Swaziland	-	-	-	50	?	50?
Transkei	-	-	-	500	363	400
Transvaal	-	-	-	2000	1300	1500
Zimbabwe	-	-	240	-	?	?
"Totals"	10 000	2500	10 000	3700	1900	2500

Notes on totals:

1) King (1981) based on Mundy (1977 *in litt.*).
2) Collar & Stuart (1985) totals come from Mundy (1984 *in litt.*)
3) Brooke (1984a) total is the minimum number for South Africa and Lesotho only.
4) Brooke (1984b) is based on Mundy (1982 *in litt.*), and the total is the minimum number for South Africa, Swaziland and Lesotho only.

Table 2.2
Summary of Cape Vulture population estimates

Author	Estimated No. pairs	Date of estimate	Comments
King (1981)	2500	1977	
Brooke (1984a)	1900	1982	South Africa + Lesotho
Brooke (1984b)	2500	1982	Ditto + Swaziland
Collar & Stuart (1985)	3700	1984	

At the end of the 1970s there were just over 90 sites in the Cape Province which were known to be Cape Vulture roosts or colonies, or were once suspected of being roosts or colonies, or were vulture place names (e.g. Aasvogelvlei, Xalanga; Boshoff & Vernon 1980). In the early 1980s a list of just over 110 such Cape Vulture sites was produced for all of southern Africa (P.J. Mundy pers. comm.). At the turn of the century reductions in Cape Vulture numbers as well as a reduction in range had been noted. It was only with the 1965 Cape Nature Conservation survey that the first real concern was expressed about the serious decline in Cape Vulture numbers. This refrain was taken up in two *Red Data Books* in the 1970s (one local: Siegfried, Frost, Cooper & Kemp 1976, and one international: King 1981) in which the species was rated as 'vulnerable'. This concern increased in the 1980s following two more *Red Data Books* (one local: Brooke 1984b and one for Africa: Collar & Stuart 1985) in which the ratings were 'vulnerable' and 'rare'.

During the 1980s a number of population estimates were made (Table 2.1), based more on educated guesses than on direct counts. The total number of birds estimated from these counts shows an increase with time (Table 2.2) but this is thought to reflect improved estimates, rather than a real increase. Reliable counts have been made for some regions, the most important being for the Transvaal (Benson, Tarboton, Allan & Dobbs 1990) in which these authors put the number of breeding pairs at 3000 and rate the numbers breeding over the period 1980-1985 as stable.

2.4 Breeding[4]

A working hypothesis of this thesis is that Cape Vultures form strictly monogamous pairs for life, stay at a particular colony (though not necessarily their natal colony) and can start to breed somewhere between their fourth and sixth years. About 80% of previously used nests are reused in any given year and it is estimated that about 85% of pairs breed in a given year, i.e. missing about one year in seven, on average.

The breeding season begins on about 10 April in the northern colonies getting latter as one proceeds south, the latest median egg-laying date at a colony is about 20 June at Potberg. Egg laying at any given colony is synchronized, with the bulk of eggs being laid in about four weeks. Usually only one egg is laid. Occasionally two have been found in a nest, but there is only one record of a two-egg clutch giving rise to large nestings. Egg mass is about 250 g, which is about 2.7% of female mass. Incubation is by both parents. Because of this narrow window in which new individuals are added to the population, it can be modelled as a 'birth pulse'.

Eggs can be lost to predators and Black Eagles *Aquila verreauxii*, Whitenecked Ravens *Corvus albicollis* and Chacma Baboons *Papio ursinus* have been implicated. Breeding success, measured as eggs producing large fledglings, can be as high as 75% at undisturbed colonies. Thus the maximum fecundity is $(0.85)*(0.75)/2=0.31875$ (i.e. about 0.32) large female fledglings per breeding pair p.a.

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[4] See Mundy, Butchart, Ledger & Piper (1992 p. 88-96).

Once hatched, nestlings are closely brooded, but after some ten days the parent sits a little higher, off the nestling. Both parents brood and bring food, seemingly in equal proportion. At 60 days a nestling needs an average of about 900 g of fresh meat per day and this increase to an average of about 1100 g per day at age 80-85 days. This is a 'bottleneck' period for the adults. With one adult on the nest protecting the nestling and the other out foraging, parents are able to feed only every second day. Given their maximum crop-size of 1500 g, this is not enough food to sustain them while they feed the nestling. By analogy with studies in East Africa, it is probable that the adults lose body mass and condition in this 30 day period. This bottleneck limits the productivity to one large fledgling per pair p.a. Nestlings are vulnerable to predation from Black Eagles and Whitenecked Ravens and possibly Chacma Baboons. The nestling period lasts about 140 to 150 days, though some individuals stay longer.

Eggs laid in mid-May will produce fledglings in mid-November while mid-June eggs will yield fledglings in mid-December. Thus all colonies should have their nestlings fledged by the end of the calendar year in which the eggs were laid. This suggests that the year-end is a suitable time for placing the 'nominal' birth-pulse in the demographic models.

The post-fledging dependence period (PFDP) is variable, lasting from 15 to 221 days with an average of 114 days. During the PFDP the fledgling is still fed by its parents at a rate of about once per 3.5 days - but only if the fledgling comes to its nest site, when the parents are there. Adults will not feed their own fledgling away from the nest site and will not feed other fledglings if they come to the nest site. By the time the next breeding season starts, all the previous year's fledglings have ceased coming to their natal nest site, and are independent of their parents (or dead).

2.5 Survival and causes of mortality[5]

Once fledglings leave the safety of the area around their nest, they are subjected to many dangers. Some of these are natural, having impacted on the species since time immemorial, while others are unnatural, the result of environmental changes brought about by modern human society. These mortality factors are listed and briefly described below. There are no estimates of the impacts which any of the factors may have had on the Cape Vulture's population. Lastly such estimates of survival as are available are listed and described.

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[5] See Chapter Nine in Mundy, Butchart, Ledger & Piper (1992).

Unnatural mortality.

Six major causes of unnatural mortality have been observed to impact on Cape Vultures.

1) Disturbance and persecution. Unintentional disturbance has been caused by military and other aircraft flying past colonies and thereby initiating 'fly-outs', which can result in eggs and nestlings being left unguarded and vulnerable to attack. Unintentional disturbance from climbers, hikers, 'day-trippers' and passing motor vehicles (especially noisy motorcycles) can have the same effect. Deliberate disturbance at colonies is caused by those who roll rocks down the face of the cliff (they may claim to be bored) or researches who fire a gun at the foot of a cliff so as to count the number of roosting birds more easily (Jarvis, Siegfried and Currie 1974)! Persecution by persons using vultures for target practice has been recorded, as well as by egg collectors and those wanting to kill them for subsequent sale and use in the traditional medicine trade. Vultures have been deliberately killed by boys using home-made bombs. In the various war-zones around southern Africa, vultures of a number of species have been killed after detonating antipersonnel mines. Vultures have also been killed by passing vehicles, while feeding from road-kills.
2) Collisions. Vultures collide in flight with aircraft, overhead power lines, communication masts (and the stay-wires that support them) and fences. This often happens in misty weather, especially when these structures have been placed on the hilltops near vulture roosts or colonies. Sometimes collisions with overhead power-lines are misreported as electrocutions, so that this phenomenon may be underreported.
3) Poisoning. Incidents of death caused by deliberate and accidental poisonings have been reported. Vultures have often been perceived as 'problem animals' along with Lion, jackals, hyenas, African Wild Dog, Caracal and domestic dogs. They have been deliberately poisoned by placing some dangerous substance in a dead animal, put out as bait. The list of poisons used is long and includes 1080, strychnine, Curatter, Dieldrin and Toxaphene as well as various organophosphorus pesticides. Often the target 'problem animal' is not a vulture, but vultures are killed anyway. Accidental poisoning is widespread with the use of an increasingly wide variety of agricultural chemicals these include insecticides, acaricides and the like (e.g. Coopex, Lujet, Dazzel and Folidol). Two supposedly target-specific devices for combating small problem animals (mainly jackals) have been developed in North America: the toxic collar and the 'coyote-getter'. Unfortunately both have been shown to be dangerous to vultures and have killed a considerable number in southern Africa. There are no estimates of the effects of poisoning on vultures in southern Africa, but it is strongly suspected that the originally 800-strong Cape Vulture colony at Karringmelkspruit declined to extinction over a period of 25 years as a result of poisons used in the surrounding environment. It is also suspected that the deliberate poisoning of Cape

Vultures is slowly decreasing, but poisons are still a threat to the species, including those ingested incidentally from domestic stock. Poisoned birds sometimes fly to, and roost on, power pylons where they succumb, fall to the ground and are mistaken for electrocuted birds.

4) Electrocution. With the spread of the electricity reticulation network in southern Africa, since the Second World War, there has been a massive increase in the number of low, medium and high-tension power-lines and towers in the sub-continent. Many of the earlier designs (in the 1950s to 1970s) were not 'bird-friendly', and these killed many Cape Vultures, especially young birds. It is thought that fatalities caused by electrocution were largely confined to the southwestern Transvaal, increasing through the 1970s, peaking in the early 1980s and decreasing thereafter. The control of the problem was a direct result of a policy decision by Eskom (the southern African electricity utility corporation) to make their structures safer. It seems that electrocution is now a minor source of mortality for the Cape Vulture.

5) Drowning. Vultures drown in water troughs constructed for use by livestock, and especially in large open reservoirs which have vertical sides. This problem is widespread throughout the drier regions of southern Africa, and drownings are an ongoing source of mortality. However, when a drowning occurs, often more than one bird is killed (sometimes over 30 are found together), and this could be a catastrophe for a small isolated colony.

6) 'Food quality'. Cape Vultures, may have been feeding from the carcasses of domestic sheep and goats, in the southern Cape, for almost 2000 years, and from domestic cattle for nearly 1000 years. However, it is only in the last four centuries that these domestic stock have come to dominate the landscape to the virtual exclusion of indigenous herbivores. But these domestic stock are not just domesticated wild animals (Mundy, Butchart, Ledger & Piper 1992 p. 366):

> The modern domestic animal is no longer a simple collection of flesh, skin and bone, but a mobile pharmacological and chemical compendium. Growth stimulants, nutritional supplements, trace elements, vitamins, antibiotics, pour-on systemic acaricides, and other high-tech molecules may be present inside, or on the surface of a sheep, pig or cow that is fed on by vultures in modern Africa.

Nothing is known of the effects of these chemicals on vultures and their ability to reproduce, but it has been recorded that eggs from southwestern Cape colonies showed higher levels of organochlorines than elsewhere in the subcontinent. Of the eight species of vultures that were once widely distributed in southern Africa, only the Cape and African Whitebacked Vultures have shown any great success in transferring from wild to domestic mammals as their food-base. As a result, they now have to rely on a much narrower range of food sources. In addition, the loss of Lions and hyaenas has meant a loss of 'bone-crushing' agents which used to provide an ample supply of calcium-rich fragments that Cape Vultures could take back to their nestlings. This has resulted in a calcium deficiency which causes some nestlings to have malformed skeletons and leads to their eventual demise when they try to fly.

Natural mortality.

Even in a world free of the influence of humans and their technology, vultures would still have to face a wide range of causes of natural mortality.

1) Starvation. Young vultures are often out-competed at carcasses by adult birds, and they tend to wander away from areas dominated by adults while they seek out other food-rich regions. In so doing, they run a high chance of not finding any food at all and dying. Even if they find food, their low social status, inept feeding technique and general inexperience may prevent them from feeding adequately and so cause them to die from starvation. Undernourished birds are also susceptible to a variety of other proximate causes of mortality so that the incidence of starvation-induced deaths may not be appreciated.
2) Inexperience. Finding food is a communal activity with vultures. They form large feeding nets, watching each other watch for signs of death - other vultures or corvids on the ground, an immobile beast and so on. This must take time to learn, and the young bird is vulnerable during this learning period. Young birds are less likely to recognize dominant birds in a feeding hierarchy, and also unlikely to recognize dangerous competitors such as Lions, hyaenas, jackals and Lappetfaced Vultures. This could lead to permanent and fatal damage in an ensuing fracas.
3) Collision. Vultures have to learn to fly great distances, often under turbulent conditions. When coming in to roost in the proximity of unyielding cliff faces, they can misjudge their landing and crash into the cliff face (pers. obs.).
4) Fire. From time to time, breeding cliffs are engulfed in veld fires with the potential for loss of nests, eggs and nestlings.

Predation is unlikely to be anything other than a minor cause of death among fit, adult birds.

There is only one set of survival estimates for the Cape Vulture (Piper, Mundy & Ledger 1981), based on the recoveries of birds ringed as pulli, in which the survival of first-years was estimated to be less than 18% and recruitment to the breeding population at six years was put at 4%. These estimates were criticized (Burnham, Anderson & White 1985) because the ring-recovery process is unreliable. An additional estimate of recruitment to the breeding population was made using 44 nestlings which had been colour-ringed and later resighted in their natal colony (Robertson 1984): recruitment was estimated at 11%.

2.6 Movements[6]

Nestling Cape Vultures have been ringed at five major centres in southern Africa: the Magaliesberg, southeast Botswana, eastern Transvaal, Transkei and the southwestern Cape. These birds have been resighted and recovered all over southern Africa.

1) Colleywobbles-ringed birds have been resighted in Zimbabwe and the southwestern Cape and recovered in the eastern and northern Cape, the Orange Free State and southwestern Transvaal.
2) Botswana- and Magaliesberg-ringed birds have been recovered at almost every point of the compass, and as far afield as Namibia.
3) Eastern Transvaal birds have been recovered in the southwestern Transvaal, and resighted in Zululand and northeast Botswana.

First- and second-year birds have been seen, or recovered, up to 1200 km from the place of ringing, but adult birds have only been seen, or recovered, up to 760 km from their place of ringing.

From a preliminary inspection of these data the following general conclusions are drawn.

1) There is no evidence for migratory behaviour.
2) A Cape Vulture from any one colony in southern Africa can travel to any other part of the subcontinent, even if there are no vultures there.
3) Young birds are nomadic and visit areas not used by adult birds, the so-called 'nursery areas'. Two such areas suggested are Kimberley in the northern Cape and Wabai Hill in Zimbabwe. Nursery areas are thought to have an abundant food supply (at least for part of the year) and to be unsuitable for breeding birds on account of distance from breeding colonies.

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[6] See Mundy, Butchart, Ledger & Piper (1992 p. 82-82; 375).

2.5 Summary

The basic biology of the Cape Vulture is fairly well known. It is probably among the best-studied of the Old-World vultures. Its status and distribution are not yet well described, and this is considered a high priority - inventory is the starting point for conservation. The basic breeding biology has been documented, though the estimate of the proportion of pairs which attempt to breed in any one year is not yet established. Survival has been poorly studied, and there are no adequate estimates for age-specific survival rates or for recruitment. The causes of mortality described above can all be classified as 'short-term'. No consideration has been given to those macro-factors - especially food - which limit the distribution in some ultimate fashion. Across the subcontinent, much land has been degraded, converted to cultivation of crops, or planted with Australian and Palaearctic trees. All of this has decreased the land available for wildlife areas and pastoralism, both commercial and subsistence. Thus the food base for vultures has shrunk in recorded history, and continues to do so. The resighting of uniquely-marked birds and the recovery of ringed birds has given some insight into the way in which Cape Vultures spread themselves about the subcontinent, but as yet there are no data for assessing philopatry or colony fidelity.

One of our dreams is to be able to say with certainty: "The total Cape Vulture population consists of X birds:. Only a few species, mostly exceedingly rare, can be thus counted. However, our goal is not as far-fetched as it may seem. Cape Vulture colonies are conspicuous by virtue of the "whitewash" deposits, and with the aid of a telescope it is possible to count the birds. By knowing what proportion of the population comprises non-breeding birds (by trapping free-flying vultures), we can work out a grand total for the species. With this end in view, we have started a register of all colonies.

Ledger & Mundy (1975)

Chapter Three

Population status, distribution and trends

Contents

Abstract

Data are collated on known Cape Vulture sites: vulture place names, roosts and colonies. A total of 441 sites have been documented of which 167 are currently in use. A total of about 12 000 Cape Vultures exist in the wild including approximately 4400 breeding pairs. About 73% of the population breeds and are concentrated in two core areas: the first in Transvaal and Botswana and the second in Lesotho, Transkei, Eastern Cape and Natal. There are isolated breeding populations in Namibia and the southwestern Cape. The bird sightings data from SABAP are used to construct a distribution map using binomial kriging. It is shown that there is a good correspondence between these SABAP data and the site count data. The site count data are used to calibrate the reporting rate data and this is the first time this has been done in southern Africa. Temporal trends in attendance at 14 sites are analyses and the decreasing sites tend to be at the edge of the species' range while the stable or increasing sites are in the core areas.

Chapter Three

Population status, distribution and trends

Good demographic modelling, the object of this thesis, can be undertaken if there are reliable estimates of the major demographic parameters as well as some notion of how they vary in space and time. In this chapter, and the next three, consideration is given to estimating the following parameters.

1) The population size and composition in each region.
2) The internal gains (from births and immigration) within a region.
3) The internal losses (from deaths and emigration) within a region.
4) The fluxes between regions which make up the emigrants and immigrants.

Three approaches are used to provide these estimates: collation and interpretation of existing parameter estimates for the Cape Vulture, analysis of new data collected for this purpose, and by analogy with other well-studied species.

In ornithological circles 'status' has been defined (Weaver 1981: 111) as:

> The nature of a species' occurrence in a particular area. It denotes the frequency with which the bird is found, usually described vaguely by such terms as "common" or "scarce", and the seasonality of its use of the area, the bird being called a resident, summer visitor, winter visitor or passage migrant, as appropriate.

This definition is too vague for use in this chapter, but it will be alluded to below when discussing the sightings data from bird watchers. For this chapter, the term population status is taken, more restrictively, to mean the total size of the population and its categorization by sex and age, breeding and non-breeding. Estimates of population size, by region, come from counts of the numbers of birds using roosts and colonies. From these counts some inferences can also be drawn as to the proportion of non-breeding birds. However, there is as yet no method for sexing Cape Vultures by sight so that there are no data on the sex ratio at any stage in the species' age-pyramid. Some ageing data may be had from counts at roosts and colonies, but most of these data come from counts of birds at vulture restaurants, carcass observations, bathing and perching on electricity towers.

Distribution, or dispersion, is (Newton 1979: 38 ff.):

> ... concerned with the spacing between nests and colonies, with the size and density of colonies and with day-to-day movements of individual birds.

From a census of roosts and colonies it is possible to draw up a reasonable picture of the spatial distribution of the Cape Vulture. Using such little knowledge as is available on home range and foraging distance, it is possible to 'spread out' the roost and colony counts so as to get a rough picture of the likely spatial distribution of the Cape Vulture over the southern African sub-continent as the birds sally out on their daily foraging forays.

The term 'population trends' is used in the sense of changes in space and time. At a gross scale the patterns of colony and roost abandonment and colonization will be examined while at a fine scale the changes in attendance at individual roosts and colonies will be studied. Together these will be used to get some idea of the way the population can change in space and time.

3.1 Status

Cape Vultures are sociable and tend to roost together overnight in small to large congregations at sites which are used repeatedly. There are at least 400 sites which are currently being used, have been used, or are suspected of having being used in the past, by Cape Vultures as roosts or colonies. This makes almost complete enumeration possible. In the course of this study many such sites have been visited by Vulture Study Group members, and the number of roosting birds and breeding pairs counted. The census and documentation of these sites, together with a much greater number of observations from other observers have been collated and will be published elsewhere (Piper, Mundy & Vernon in prep.). Their report is hereafter referred to as the 'Site Register'. That report is so large (in excess of 500 pages) that only the briefest summary can be presented in this thesis. The reader is requested to consult that document for verification of the summaries presented below and for background information.

3.1.1 Numbers of Cape Vultures

The Cape Vulture has been reported from 13 regions of southern Africa: Botswana, Cape Province, Lesotho, Mozambique, Namibia, Natal, Orange Free State, Swaziland, Transkei, Transvaal, Zaire, Zambia and Zimbabwe. Three of these regions (i.e. Swaziland, Zaire and Zambia) have no active roosts or colonies and so will not be discussed further. There are no substantive data for the single site in Mozambique so that it too is omitted from these discussions. Only the active sites in the other nine regions are described below.

In the summaries below the following terms are used:

Site: A place where it is suspected that Cape Vultures have roosted or bred. Each site is given a unique (but arbitrary) number.

Roost: A place to which Cape Vultures regularly return to overnight; usually a cliff face.

Colony: A place where Cape Vultures definitely build nests and lay eggs as part of breeding; always a cliff face.

Documented: A site is rated as 'documented' once it has had a Colony Documentation form filled in and entered onto the Site Register (i.e. Piper, Mundy & Vernon in prep.).

Name: Each site is given a unique name by which it is referred.

Coordinates: ('Coords' in Tables). Geographical co-ordinates as degrees and minutes south and east, i.e. as DDMMDDMM.

Birds: ('No. birds' in Tables). Estimated total number of birds roosting at the site as of the last visit.

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Cape Vultures are sociable and tend to roost together overnight in small to large congregations at sites which are used repeatedly. There are approximately 441 sites which are currently being used, have been used, or are suspected of having being used in the past, by Cape Vultures as roosts or colonies. This makes almost complete enumeration possible. In the course of this study many such sites have been visited by Vulture Study Group members, and the number of roosting birds and breeding pairs counted. The census and documentation of these sites, together with a much greater number of observations from other observers have been collated and will be published elsewhere (Piper, Mundy & Vernon in prep.). Their report is hereafter referred to as the 'Site Register'. That report is so large (in excess of 500 pages) that only the briefest summary can be presented in this thesis. The reader is requested to consult that document for verification of the summaries presented below and for background information.

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Coordinates: ('Coords' in Tables). Geographical co-ordinates as degrees and minutes south and east, i.e. as DDMMDDMM.

Birds: ('No. birds' in Tables). Estimated total number of birds at the site as of the last visit, this includes birds breeding as well as roosting.

Pairs: ('No. pairs' in Tables). Estimated total number of pairs breeding during the last year in which the colony was visited, usually estimated from number of active nests.

Last visit: Year during which the last assessment of the site was made.

Population trend of Pairs: ('Trnd pair' in Tables). Population trend of the number of breeding pairs at the colony. The following codes are used:

Code	*Category*
?	Unknown.
N/A	Not applicable.
+ +	Increasing strongly, at least 5% per annum.
+	Increasing, <5% p.a.
+/-	Constant, or constant with fluctuations.
-	Decreasing, <5% p.a.
- -	Decreasing strongly, at least 5% per annum.

Site type: Sites are classified as:

Unknown	No data
Abandoned	Known to have been used in the past.
Roost	Used for 'loafing' and 'over-nighting' but not for breeding.
Satellite	Secondary site, peripheral, small, short-lived or seldom used breeding colony.
Nucleus	Primary, core breeding colony in existence for some time.

The spatial location of nucleus and satellite colonies, roost-only sites, abandoned sites and sites of unknown status are shown graphically (Figures 3.1 to 3.5).

Assessment certainty: The certainty of the authors' assessment of numbers, breeding and population trend; subjectively rated as:

Unknown	No data
N/A	Not applicable
Low	Little knowledge of site
Moderate	Fairly well known
Sure	Well known

Botswana

Botswana has ten Cape Vulture sites and all of these have been documented (Piper, Mundy & Vernon in prep.). Eight of these are currently active (Table 3.1). The Botswana sites have been documented in recent times[1]; two (i.e. 20%) in the period 1981 to 1985 and eight (80%) post-1985. Of the ten sites, five (i.e. 50% of 10) are nucleus, or core breeding colonies, one (10%) is a satellite colony, two (20%) are roosts while two (20%) have been abandoned. Two of the breeding colonies are decreasing. There are just over 250 breeding pairs and about 725 birds in Botswana. These figures represent about 6% of the total breeding population and of all Cape Vultures.

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[1] Subsequent to the completion of this analysis observations of breeding and counts of attendence for most of the Botswana sites for the period 1987 to 1990, both years inclusive, have been summarised and published (Borello & Borello 1992).

Nucleus Colonies

Figure 3.1 Spatial location of all nucleus breeding colonies. Convex polygons enclose all active sites in two regions: a) Transvaal, Botswana and Zimbabwe and b) Natal, OFS, Transkei, Eastern Cape and Transkei.

All the Cape Vulture sites are in the east of the country in two clusters, one just south of the capital and the other in the Tswapong Hills. Note that there has been some switching between sites (Mundy 1983: 59-60). The Cape Vulture roosts and colonies in Botswana are so close to those in the Transvaal (see Figures 3.1 to 3.3 and 3.7) it is likely that they are subject to similar pressures from poisons, disturbance and persecution. Consequently, the populations in Botswana and the Transvaal should be treated as a single, functioning group.

Table 3.1

Active Cape Vulture roosts and colonies in Botswana.

Site	Name	Co-ords	No. birds	No. pairs	Last visit	Trnd pair	Site type	Assessment certainty
39	Bonwalenong	22372726	230	82	1986	-	Nucleus	Moderate
85	Kukubye	22452745	100	30	1986	-	Nucleus	Moderate
44	Mannyelanong	25042546	130	44	1986	+/-	Nucleus	Moderate
21	Manong Yeng	22402725	200	80	1986	+/-	Nucleus	Moderate
46	Manyana	24512539	10	0	1985	N/A	Roost	Moderate
64	Otse Hill	25012544	2	1	1983	N/A	Satellite	Low
29	Sebale	22322737	3	0	1986	N/A	Roost	Low
439	Seolwanc	22402741	50	20	1986	?	Nucleus	Low
		Totals	725	257				

Cape Province

Among all regions, the Cape Province has the highest number of possible Cape Vulture sites (190; Piper, Mundy & Vernon in prep.), i.e. 45% of all known sites in southern Africa, but only 15 of these are still active (Table 3.2). There are 94 sites which have been documented this century, the majority of these (55, i.e. 59% of the documented sites) were last documented at the time of the survey by Boshoff & Vernon (1980). Only 9 sites (10%) have been documented since 1980, while 30 (32%) were last assessed prior to 1976.

It is estimated that there are 109 breeding pairs of Cape Vultures in the Cape Province (i.e. 3% of all the breeding pairs in the entire population) and approximately 550 free-flying birds (i.e. 5% of the whole population). The active sites are in two groups, one in the southwestern Cape and the other in a broad band in the eastern Cape where it borders the Transkei, Lesotho and the Orange Free State (Figure 3.7). Many of the sites not now used by Cape Vultures are in the Karoo, however many of these are vulture place-names so that this may not necessarily reflect actual patterns of previous occupancy and subsequent abandonment.

Satellite Colonies

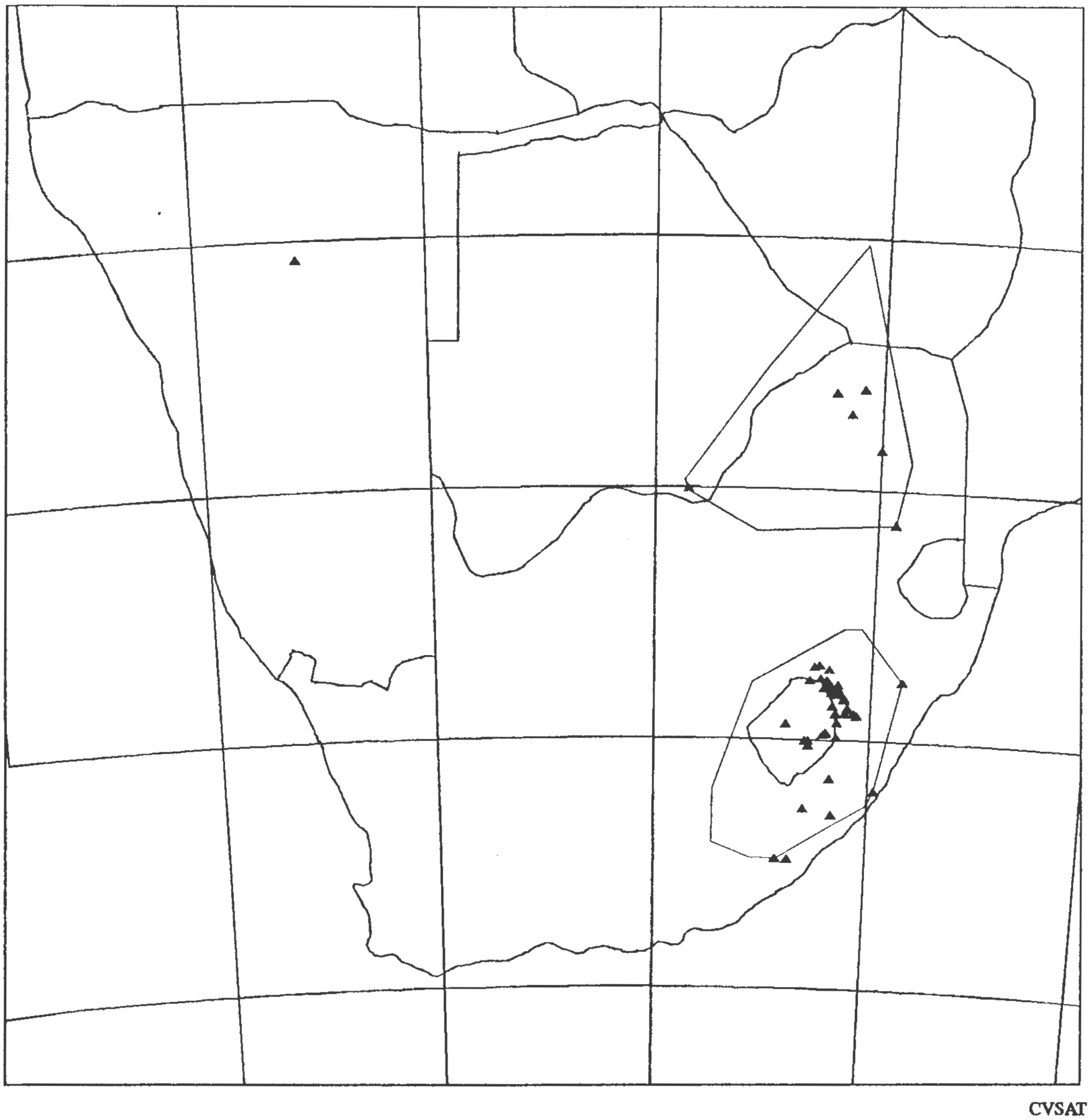

Figure 3.2 Spatial location of all satellite breeding colonies. Convex polygons enclose all active sites in two regions: a) Transvaal, Botswana and Zimbabwe and b) Natal, OFS, Transkei, Eastern Cape and Transkei.

Roost-only Sites

Figure 3.3 Spatial location of all roost-only sites (i.e. excluding active breeding colonies). Convex polygons enclose all active sites in two regions: a) Transvaal, Botswana and Zimbabwe and b) Natal, OFS, Transkei, Eastern Cape and Transkei.

Table 3.2
Active Cape Vulture roosts and colonies in the Cape Province.

Site	Name	Co-ords	No. birds	No. pairs	Last visit	Trnd pair	Site type	Assessment certainty
28	Aasvogelsberg	30572644	40	0	1979	?	Roost	Moderate
8	Aasvogelvlei	33522140	27	11	1987	+/-	Nucleus	Moderate
10	Balloch	30442743	70	25	1986	+/-	Nucleus	Moderate
233	Bellona	30552629	50	0	1976	N/A	Roost	Low
15	Forest Range	32072719	20	5	1978	-	Nucleus	Moderate
192	Gxabenya	31482658	15	0	1976	N/A	Roost	Low
16	Inverket	32122725	35	0	1978	N/A	Roost	Moderate
31	Karnmelkspruit	30512714	120	58	1986	-	Nucleus	Moderate
37	Langkloofspruit	31092802	15	0	1985	N/A	Roost	Moderate
47	Martha & Mary	32052622	40	0	1979	N/A	Roost	Moderate
60	Nonesi Nek	31502659	10	0	1972	N/A	Roost	Low
69	Perdeberg	33572132	25	0	1984	N/A	Roost	Moderate
68	Potberg	34222033	40	10	1987	-	Nucleus	Moderate
234	Rooipoort	30592623	30	0	1976	N/A	Roost	Moderate
17	Stonehenge	32222716	15	0	1979	N/A	Roost	Moderate
		Totals	552	109				

The current disjoint spatial distribution represents the effects of range contraction (Boshoff & Vernon 1980) which has given rise to the isolated southwestern Cape population. All the sites are small, most of them composed of non-breeding birds. The proportion of breeding birds is 39%, which puts the Cape in the category of a 'non-breeding' region (see Table 3.10 below and the associated discussion). With the exception of Namibia, a higher proportion of known breeding colonies have been abandoned in the Cape than in any other region. This is also true for roost-only sites (Figure 3.4). There are two temporal aspects which are worthy of consideration. First, there has been a zone of range contraction from the northern Cape and Karoo. Even if it is argued that the previous use of this vast region was sporadic, it is unlikely that this region will ever be used again if the Cape Vulture population remains at its current level. Secondly more than half of the breeding colonies and roost-only sites have declined, or are declining.

There are at most four breeding colonies left in the Cape Province (Table 3.2)[2], there are many abandoned sites in the Province (Figure 3.4) and the species has suffered at a major range contraction in the last half-century (Boshoff & Vernon 1980). Hence, the Cape Vulture now maintains, at best, a vestigial presence in its ancestral home and is likely to go extinct in the Cape Province, by the end of the century, if the current population trend continues.

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[2] However, since the completion of the above analysis two of these have ceased to function as breeding colonies: Aasvogelvlei (A.F. Boshoff pers. comm.) and Karnmelkspruit (C.J. Vernon pers. comm.).

Lesotho

In the mountain Kingdom of Lesotho there are a total of 49 possible Cape Vulture sites (Piper, Mundy & Vernon in prep.) and all have been documented. Of these 30 are currently active (Table 3.3). Because of the intensive investigation by T.J. Donnay (loc. cit.) it is possible to state that 36 of the sites (i.e. 74% of 49) were last visited post-1985 while nine (18%) were visited in the period 1980 to 1985 with only two (4%) having been last visited before 1980; two sites (4%) have as yet to be visited. Of the 49 Cape Vulture sites in Lesotho 23 are currently breeding colonies. Thirteen of the sites (i.e. 27% of 49) are nucleus, or core breeding colonies while 10 (20%) are satellite colonies. There are 12 roost (24%) and two sites (4%) which have been abandoned. The current types for 12 sites (25%) can not be determined, though some may be active colonies or roosts.

From the earlier work of J. Jilbert and the 1984 to 1986 field surveys of T.J. Donnay (loc. cit.) it is possible to assert that currently there are at least 450 breeding pairs at known sites, with about 500 pairs in total (T.J. Donnay loc. cit. suggests approximate limits of 400 to 650 pairs) estimated for the whole Kingdom. Similarly the minimum count of about 1228 birds, at known sites, indicates a probable total of 1300 (with approximate limits of 1050 to 1450). These estimates represent 10% of the breeding pairs and 10% of the world's Cape Vulture population.

The major breeding colonies are located in the central highlands and in the east. The sites in the south and west are, in the main, roosts (Figures 3.3 and 3.8).

The sites are small to medium in size and the inter-site distance varies from a few kilometres to moderate distances. In the opinion of T.J. Donnay (pers. comm.), sites along the southern escarpment are used as staging posts by birds from the interior which forage in Natal and Transkei. It is also interesting to note that all the breeding colonies are on basalt formations, none are on sandstone; there are only roosts on sandstone cliffs (this is contrasted with the situation in Natal: Brown & Piper 1988). There are too few data on age composition to make any meaningful remarks on age-distribution within Lesotho. The proportion of breeding birds is 74.4% which is just above the average of 73.3% for the entire population, putting Lesotho in the category of regions called 'breeding' (see Table 3.10 below and the associated discussion).

Abandoned Sites

Figure 3.4 Spatial location of all abandoned sites. Convex polygons enclose all active sites in two regions: a) Transvaal, Botswana and Zimbabwe and b) Natal, OFS, Transkei, Eastern Cape and Transkei.

Sites of Unknown Status

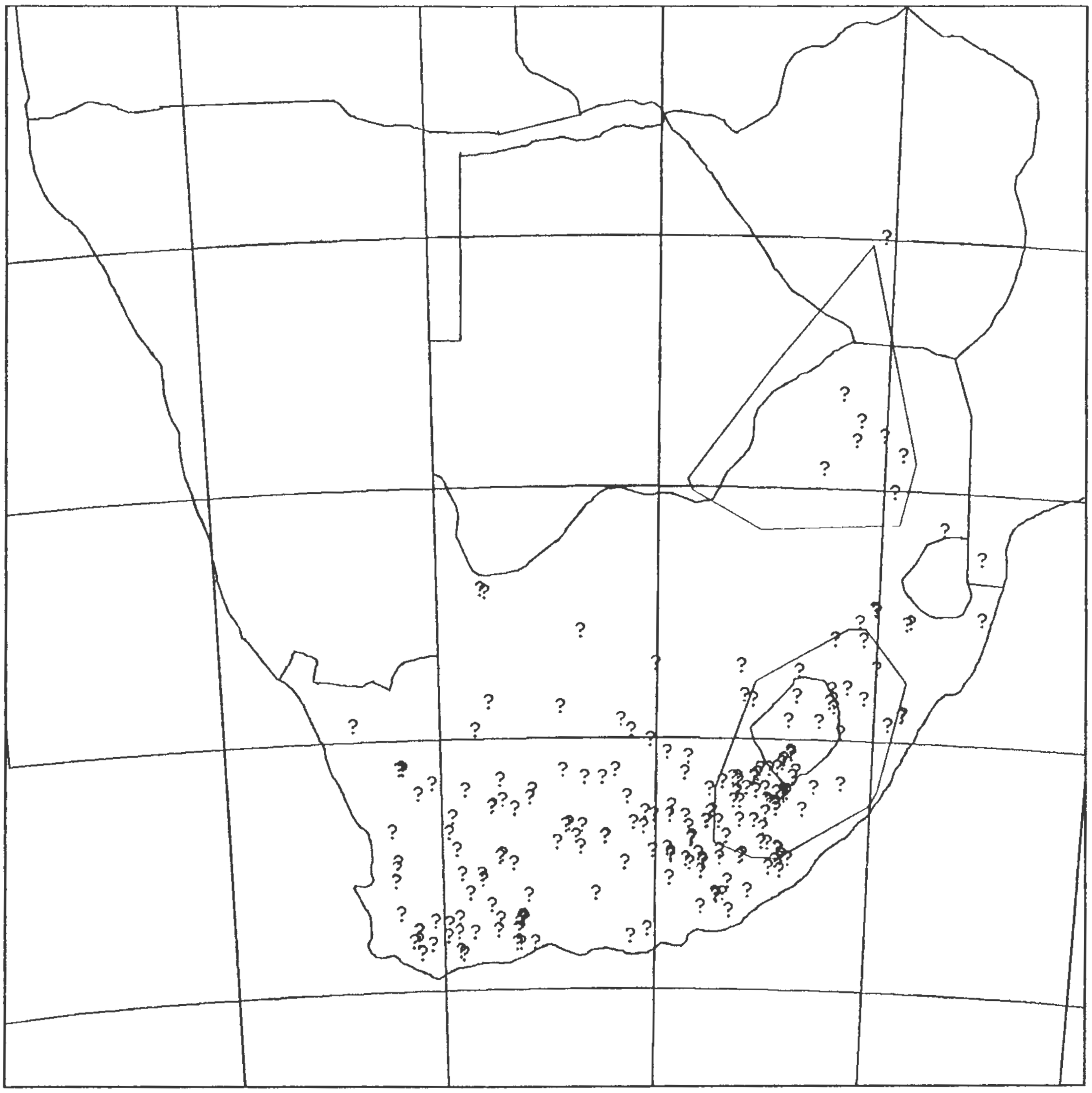


Figure 3.5 Spatial location of all putative sites of unknown status. Convex polygons enclose all active sites in two regions: a) Transvaal, Botswana and Zimbabwe and b) Natal, OFS, Transkei, Eastern Cape and Transkei.

Nine of the breeding colonies have enough historical data to assess population trends. Of these sites seven (i.e. 78% of 9) are stable or show fluctuations about a constant value while two (33%) are declining, one of them rapidly (Semonkong). The sites in the south and west are used, mainly, as roosts and many of these are declining, while some are only used sporadically. Nearly all the sites in the north and in the lowlands, known from historical records, are either abandoned or are declining roosts. When looked at in terms of the number of breeding pairs, 330 pairs (ca. 73%) are at stable colonies, 53 pairs (ca. 12%) are at declining colonies, while 68 pairs (ca. 15%) are at colonies of unknown status.

Lesotho forms an altitudinal enclave within the Cape Vulture distribution and accounts for a tenth of the total population. It is likely that those Cape Vultures roosting and breeding along the Natal-Lesotho Drakensberg forage in regions similar to those of Lesotho and the two regions may form a single unit and possibly should be treated as such.

Table 3.3

Active Cape Vulture roosts and colonies in Lesotho.

Site	Name	Co-ords	No. birds	No. pairs	Last visit	Trnd pair	Site type	Assessment certainty
313	Bolahla	29062818	25	10	1986	+/-	Nucleus	Moderate
175	Devil's Knuckles,Sth	29522906	10	0	1986	N/A	Roost	Moderate
314	Khora-ea-Mokhooa	29052819	80	35	1985	?	Nucleus	Moderate
315	Khubelu	28572854	25	8	1986	?	Satellite	Low
178	Koakoatsi River,Srce	28582904	21	6	1982	?	Satellite	Low
312	Lehaha-la-Molapo	29082821	60	25	1985	?	Nucleus	Low
221	Litsoene	29502820	5	0	1986	?	Roost	Low
318	Lower Moremoholo	29142904	60	25	1986	+/-	Nucleus	Low
217	Mafeteng Maboloka Mn	29542718	2	0	1986	N/A	Roost	Low
213	Maqhaba	30072834	25	10	1986	?	Roost	Low
215	MaraKabei Manong	29412803	15	5	1986	?	Satellite	Low
320	Maseepho	30012835	30	10	1986	?	Satellite	Moderate
219	Matebeng Pass	29532855	15	5	1986	?	Satellite	Low
50	Mechachaneng	28402840	75	25	1986	+/-	Nucleus	Moderate
179	Metebong-ea-lelingoa	28582856	30	10	1986	+/-	Nucleus	Low
317	Mohlokohloko	29412854	80	25	1986	?	Nucleus	Low
53	Mokhotlong	29192906	65	30	1982	?	Satellite	Low
316	Monyetleng	29412852	125	45	1986	?	Nucleus	Low
55	Moteng Pass	28482834	25	10	1986	?	Satellite	Low
91	Quthing Valley,Upper	30202809	125	55	1986	+/-	Nucleus	Moderate
26	Seforong	30212806	80	40	1986	?	Nucleus	Low
195	Sehlabathebe	29502907	5	0	1986	N/A	Roost	Moderate
176	Sehonghong River	29282911	10	5	1986	-	Satellite	Moderate
77	Semonkong	29532804	45	10	1986	- -	Nucleus	Moderate
216	Tenane	29342828	15	0	1986	N/A	Roost	Low
214	Thaba-Matseka	30012830	20	8	1986	?	Satellite	Low
83	Thaba-Tseka	29272833	50	20	1986	+/-	Nucleus	Moderate
319	Tlhayaku	29032904	10	5	1986	?	Satellite	Low
321	Upper Senqu	29052902	20	0	1986	?	Roost	Low
67	Vulture's Peak	29072816	75	30	1985	+/-	Nucleus	Moderate
		Totals	1228	457				

All Sites

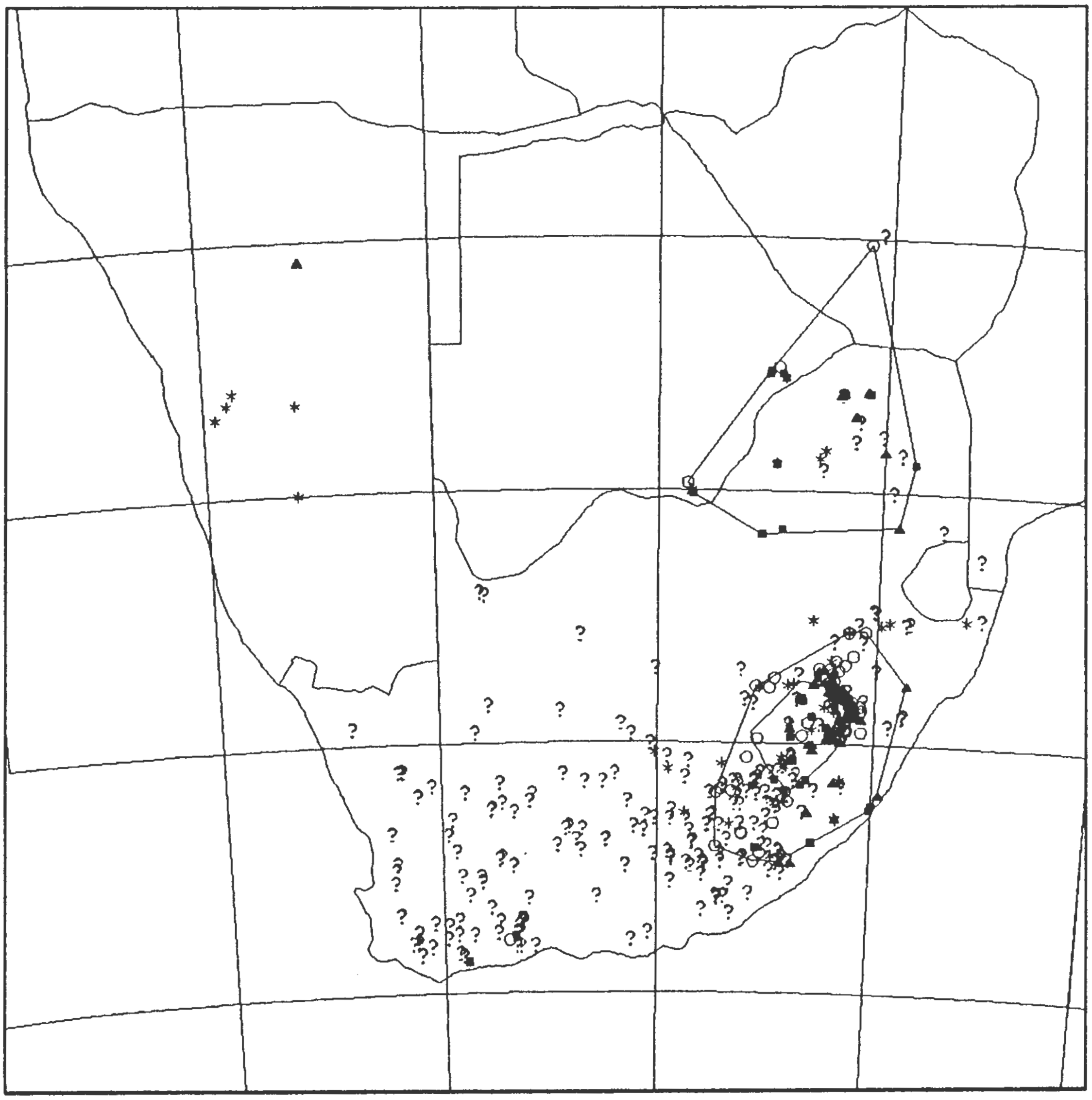


Figure 3.6 Spatial location of all putative Cape Vulture sites. Convex polygons enclose all active sites in two regions: a) Transvaal, Botswana and Zimbabwe and b) Natal, OFS, Transkei, Eastern Cape and Transkei.

Active Sites

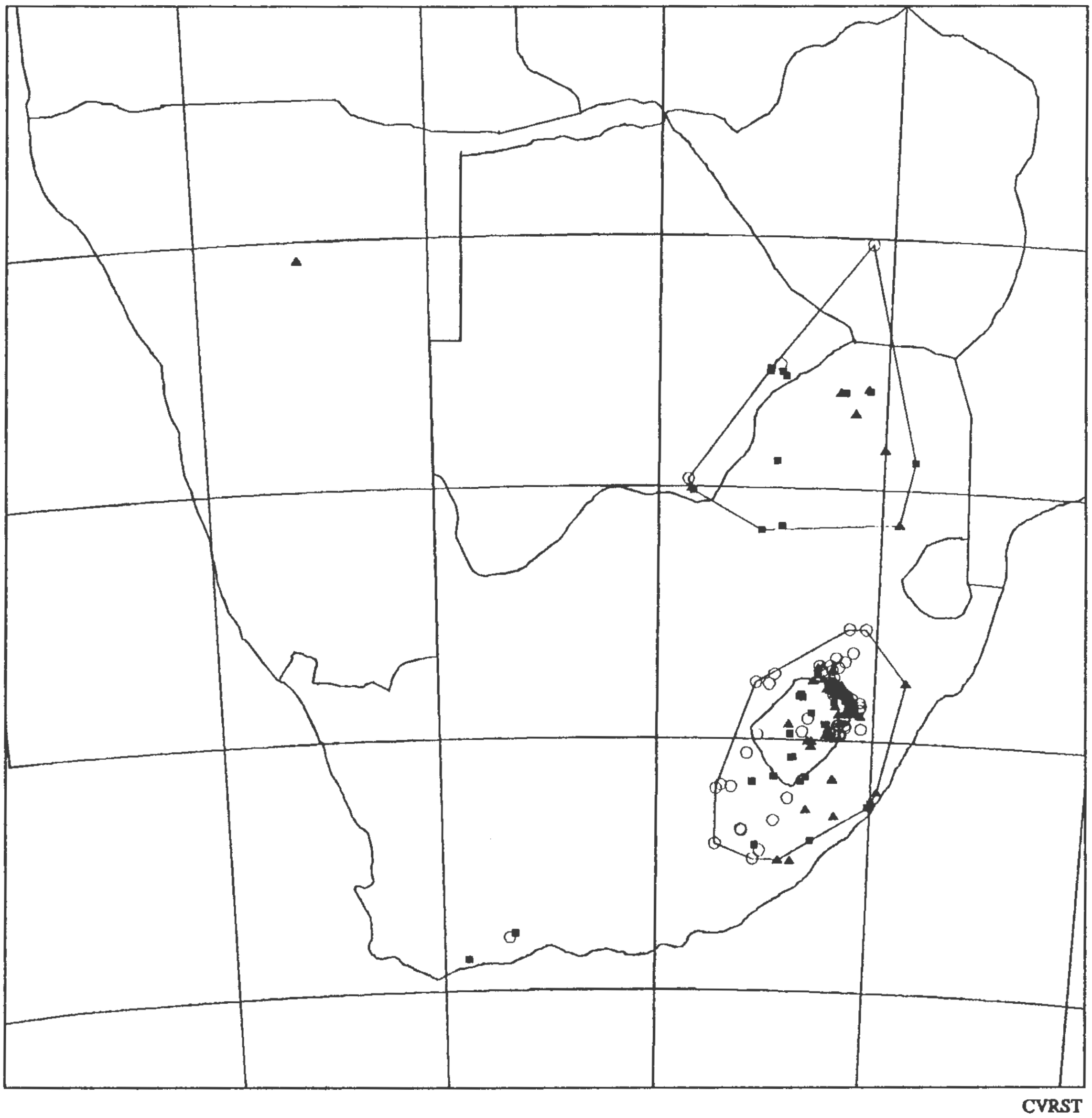


Figure 3.7 Spatial location of all active sites (i.e. roosts and colonies). Convex polygons enclose all active sites in two regions: a) Transvaal, Botswana and Zimbabwe and b) Natal, OFS, Transkei, Eastern Cape and Transkei.

Namibia

Seven possible Cape Vulture sites have been mooted for Namibia and all of these sites have been afforded some documentation (Piper, Mundy & Vernon in prep.); only one site is still active (Table 3.4). There are, as of the last count in 1988, 18 Cape Vultures in Namibia, including five breeding pairs (Brown & Jones 1989); these birds constitute 0.1% of the total population, and 0.15% of breeding pairs. Occasionally stray Cape Vultures are seen in the Etosha National Park (Brown 1985), thus the Namibian population may currently exceed 20. All the known sites are located in the central highlands and along the desert escarpment (i.e. Pro-Namib). There is little evidence that they ever extended into the Namib desert itself.

The population has undergone a dramatic decline since the 1940s (Brown 1985:11, 14). The major reasons for this decrease have not been proven but there is little doubt that the widespread and indiscriminate use of poison for the control of putative 'problem carnivores' in the commercial farming sector has had a severe and depressive effect on many scavengers. It has also been hypothesized that the tremendous increase in bush encroachment (a direct result of overstocking) has had the result that any large herbivores which die are not available to avian scavengers because:

1) The vultures cannot see the carcasses under the bushes and trees.
2) Even when they can see a carcass there is not enough open space for them to land between the trees and later to take off (loc. cit.).

It is likely that the one remaining site will continue to grow only if it is provisioned and protected (Brown & Jones 1989). The extensive and effective education and raptor-information programmes (mounted by the Namibian Department of Nature Conservation) are having a positive effect on the survival of Cape Vultures, the other vulture species, and raptors generally in Namibia (C.J. Brown pers. comm.).

Table 3.4
Active Cape Vulture colony in Namibia.

Site	Name	Co-ords	No. birds	No. pairs	Last visit	Trnd pair	Site type	Assessment certainty
100	Waterberg	20221712	18	5	1988	+	Satellite	Moderate

Natal Province

A total of 91 Cape Vulture sites have been mooted for Natal and of these 80 (i.e. 88% of 91) have been documented while 11 (12%) have not; of these 76 are currently active (Table 3.5). Only three sites (i.e. 3.3% of 91) have been documented since 1985; the vast majority (i.e. 76 ≈ 84%) having been documented by C.J. Brown in the early 1980's (Brown & Piper 1988). There are two sites which were documented prior to 1980 (2.2%) and 10 sites (11%) of unknown date.

Of the 91 Natal sites 72 (i.e. 79%) were documented by C.J. Brown at least once and of these 68 were not visited by any one else (see Piper, Mundy & Vernon in prep.). In order to harmonize the census technique of C.J. Brown with that used here, the following assumptions are made:

1) A site rated as 'permanent' and counted once by C.J. Brown is assigned to the category 'roost'.
2) If the site was counted more than once, and the individual counts are known then they were examined to determine if any assessment of population trend could be made.
3) A site rated as temporary and counted once only was assessed as a 'roost' with a 'low' certainty.
4) If a site was counted more than once then an average value was assigned to the population at that site.
5) The number of breeding pairs was set equal to the number of nests counted because there is, as yet, no measure of the proportion of adults who breed every year.

There are 25 putative breeding colonies in Natal and all of these are rated as satellites. Of the remaining 66 sites 52 are considered to be roosts, while three have been abandoned and no type was allocated to the other 12 sites. The satellite breeding colony at Umtamvuna is rated as stable; this lack of assessment of population trends for this region is due to so few sites having been monitored over any length of time.

Natal has about 270 breeding pairs which constitute 6% of the whole breeding population and approximately 1500 Cape Vultures representing 13% of the total population. However, Brown & Piper (1988) estimate that there are about 325 breeding pairs along the Natal and Lesotho Drakensberg escarpment. Thus the total breeding population for Natal is probably just over 400 pairs.

Breeding Colonies

Figure 3.8 Spatial location of all active breeding colonies (= nucleus+satellite). Convex polygons enclose all active sites in two regions: a) Transvaal, Botswana and Zimbabwe and b) Natal, OFS, Transkei, Eastern Cape and Transkei.

Table 3.5

Active Cape Vulture roosts and colonies in Natal.

Site	Name	Co-ords	No. birds	No. pairs	Last visit	Trnd pair	Site type	Assessment certainty
153	Abbey	29512858	40	12	1983	?	Satellite	Low
158	Babangibone	28352859	36	0	1983	N/A	Roost	Low
171	Bamboo Mountain	29442921	10	0	1983	N/A	Roost	Low
125	Bannerman Face	29162927	3	0	1983	N/A	Roost	Low
121	Carbineers Wall	29192927	10	0	1983	N/A	Roost	Low
133	Champagne Castle	29062921	5	0	1983	N/A	Roost	Low
141	Cockade and Elephant	28582909	53	23	1983	?	Satellite	Low
103	Devil's Knuckels,Nth	29502907	2	0	1983	N/A	Roost	Low
162	Eastman's Peak	29022917	33	0	1983	N/A	Roost	Low
163	Enjesuthi Cottage	29082928	58	0	1983	N/A	Roost	Low
20	Episweni Mtn.	28483042	10	4	1986	?	Satellite	Low
152	Fangs, North	29522859	20	4	1983	?	Satellite	Low
151	Fangs, South	29522859	15	3	1983	?	Satellite	Low
161	Ganabu	28572913	25	3	1983	?	Satellite	Low
119	Giant's Castle	29212929	16	0	1983	N/A	Roost	Low
167	Gladstone's Nose	29452942	10	0	1983	N/A	Roost	Low
134	Gray's Pass	29042920	7	0	1983	N/A	Roost	Low
126	Gypaetus Point	29152926	6	0	1983	N/A	Roost	Low
155	Icidi Stream,Source	28492857	6	0	1983	N/A	Roost	Low
190	Ingwe 8547	28342901	58	8	1988	?	Satellite	Low
114	Ka-Masihlenga	29242926	7	0	1983	N/A	Roost	Low
111	Ka-Ntuba Pass,North	29312918	7	0	1983	N/A	Roost	Low
110	Ka-Ntuba Pass,South	29322918	4	0	1983	N/A	Roost	Low
122	Kambule	29192927	5	0	1983	N/A	Roost	Low
169	Kumulungana	29302941	129	23	1983	?	Satellite	Low
168	Kwatabamnyama	29272937	47	12	1983	?	Satellite	Low
170	Little Bamboo Mtn	29422918	8	0	1983	N/A	Roost	Low
120	Long Wall	29202927	36	3	1983	?	Satellite	Low
117	Loteni Pass	29222927	12	2	1983	?	Satellite	Low
118	Loteni River,Source	29222927	13	0	1983	N/A	Roost	Low
109	Manguan Pass	29332918	6	0	1983	N/A	Roost	Low
154	Mbundi River,Source	29512858	2	0	1983	N/A	Roost	Low
112	Mlahlangubo Pass	29282924	7	2	1983	?	Satellite	Low
142	Mlambonya Buttress	28562905	3	0	1983	N/A	Roost	Low
107	Mlanlangubo River	29392914	11	3	1983	?	Satellite	Low
157	Mount Amery	28462857	3	0	1983	N/A	Roost	Low
156	Mount Dompie	28472858	31	9	1983	?	Satellite	Low
123	Mount Durnford	29182927	5	0	1983	N/A	Roost	Low
124	Mount Erskine(A)	29172927	5	0	1983	N/A	Roost	Low
166	Mount Erskine(B)	29222939	8	0	1983	N/A	Roost	Low
56	Mount Lebanon	29182941	15	0	1983	N/A	Roost	Low
173	Mount Sutherland	29532914	11	0	1983	N/A	Roost	Low
144	Mweni Needle,Inner	28532902	83	21	1983	?	Satellite	Low
146	Mweni Needle,Outer,N	28522902	21	4	1983	?	Satellite	Low
145	Mweni Needle,Outer,S	28522902	4	0	1983	N/A	Roost	Low
147	Mweni Pass	28512901	2	0	1983	N/A	Roost	Low
149	Mweni Pinnacles,Cntr	28532859	12	0	1983	N/A	Roost	Low
150	Mweni Pinnacles,Nrth	29522859	11	0	1983	N/A	Roost	Low
148	Mweni Pinnacles,Sth	28532900	80	29	1983	?	Satellite	Low
172	Ndawana River,Source	29532912	24	0	1983	N/A	Roost	Low
138	Ndedema Dome	29042914	22	7	1983	?	Satellite	Low
160	Ngwavu	28522914	45	9	1983	?	Satellite	Low
136	Nkosazana	29042918	6	0	1983	N/A	Roost	Low
62	Ntabamhlope	29132939	15	0	1984	N/A	Roost	Low
159	Ntabenende	28442902	31	0	1983	N/A	Roost	Low

Table 3.5 (Continued)
Active Cape Vulture roosts and colonies in Natal.

Site	Name	Co-ords	No. birds	No. pairs	Last visit	Trnd pair	Site type	Assessment certainty
140	Organ Pipes	29012912	2	0	1983	N/A	Roost	Low
127	Popple Peak	29142925	11	0	1983	N/A	Roost	Low
113	Redi	29252926	2	0	1983	N/A	Roost	Low
105	Rhino Peak	29422909	7	0	1983	N/A	Roost	Low
143	Rockeries	28532903	15	0	1983	N/A	Roost	Low
73	Rockeries Pass	28532901	20	0	1984	N/A	Roost	Low
130	Scaly Peak	29102922	19	5	1983	?	Satellite	Low
132	Ship's Prow Pass	29062920	7	0	1983	N/A	Roost	Low
131	The Ape	29082922	10	5	1983	?	Satellite	Low
115	The Hawk	29232926	7	0	1983	N/A	Roost	Low
139	The Sphinx	29032914	4	0	1983	N/A	Roost	Low
116	The Tent	29222927	10	0	1983	N/A	Roost	Low
108	The Twelve Apostles	29352919	5	0	1983	N/A	Roost	Low
104	Thomathu, Source	29462908	15	0	1983	N/A	Roost	Low
129	Triplets	29112923	26	8	1983	?	Satellite	Low
128	Trogon Wall	29122924	16	0	1983	N/A	Roost	Low
89	Umtamvuna	31003008	80	40	1988	+/-	Satellite	Moderate
106	Umzimkulu River,SRCE	29412911	5	0	1983	N/A	Roost	Low
97	Vulture's Retreat	29042919	48	18	1983	?	Satellite	Low
137	Witch Peak	29042916	18	0	1983	N/A	Roost	Low
174	iTsolwane	29562913	37	10	1983	?	Satellite	Low
		Totals	1518	267				

Most of the Cape Vulture sites in Natal are situated along the Drakensberg range where Natal borders Lesotho and the O.F.S. There are few non-Drakensberg sites in Natal, one in the south on the Umtamvuna River, two abandoned sites along the southern end of the uLubombo Range in the north and a few sites in the central-north uplands.

The distribution of sites along Natal's Drakensberg escarpment reflects the availability of breeding sites, proximity to both the commercial small stock farms of Natal and the communal grazing lands of Lesotho, as well as providing a high-altitude 'launching pad' from which to begin their daily foraging forays (Brown & Piper 1988). These sites are noted for their small size (varying from two to twenty birds) and their close proximity one to another (ranging from 2 to 20 km). The proportion of breeding birds is low (35%) in comparison to the population as a whole (74%) indicating that this may well be a 'nursery' area (see Table 3.10 below and associated discussion). There are no data on age composition but it is likely that there will be a high proportion of non-adult birds in Natal. The Cape Vultures in the Lesotho and Natal Drakensberg are noted for the fact that they are considerably bigger and heavier than individuals of this species examined elsewhere (Brown 1987).

Population trends at Roosts

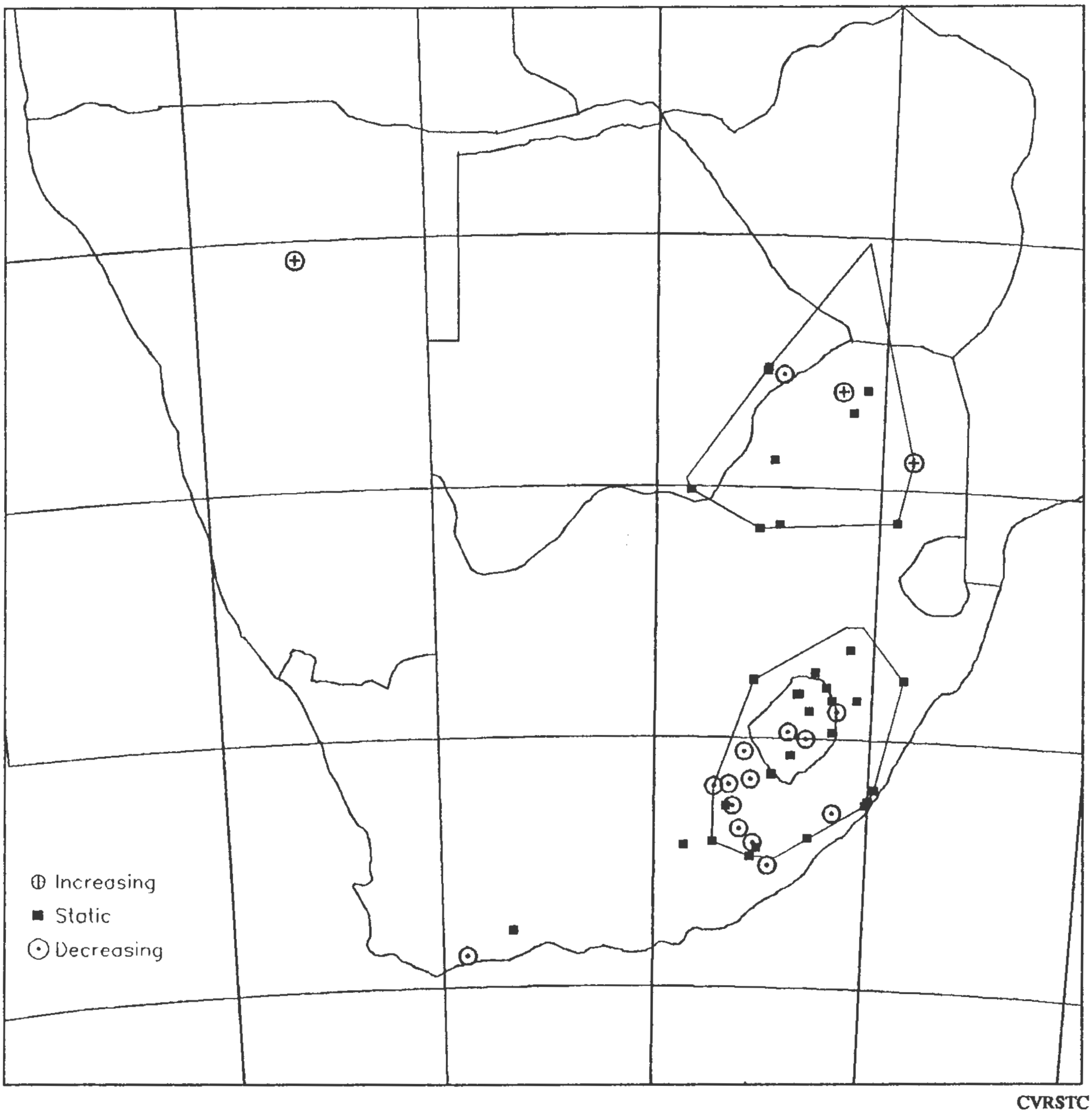


Figure 3.9 Spatial location of all active roosts for which there is an assessment of change. Convex polygons enclose all active sites in two regions: a) Transvaal, Botswana and Zimbabwe and b) Natal, OFS, Transkei, Eastern Cape and Transkei.

Population trends at Colonies

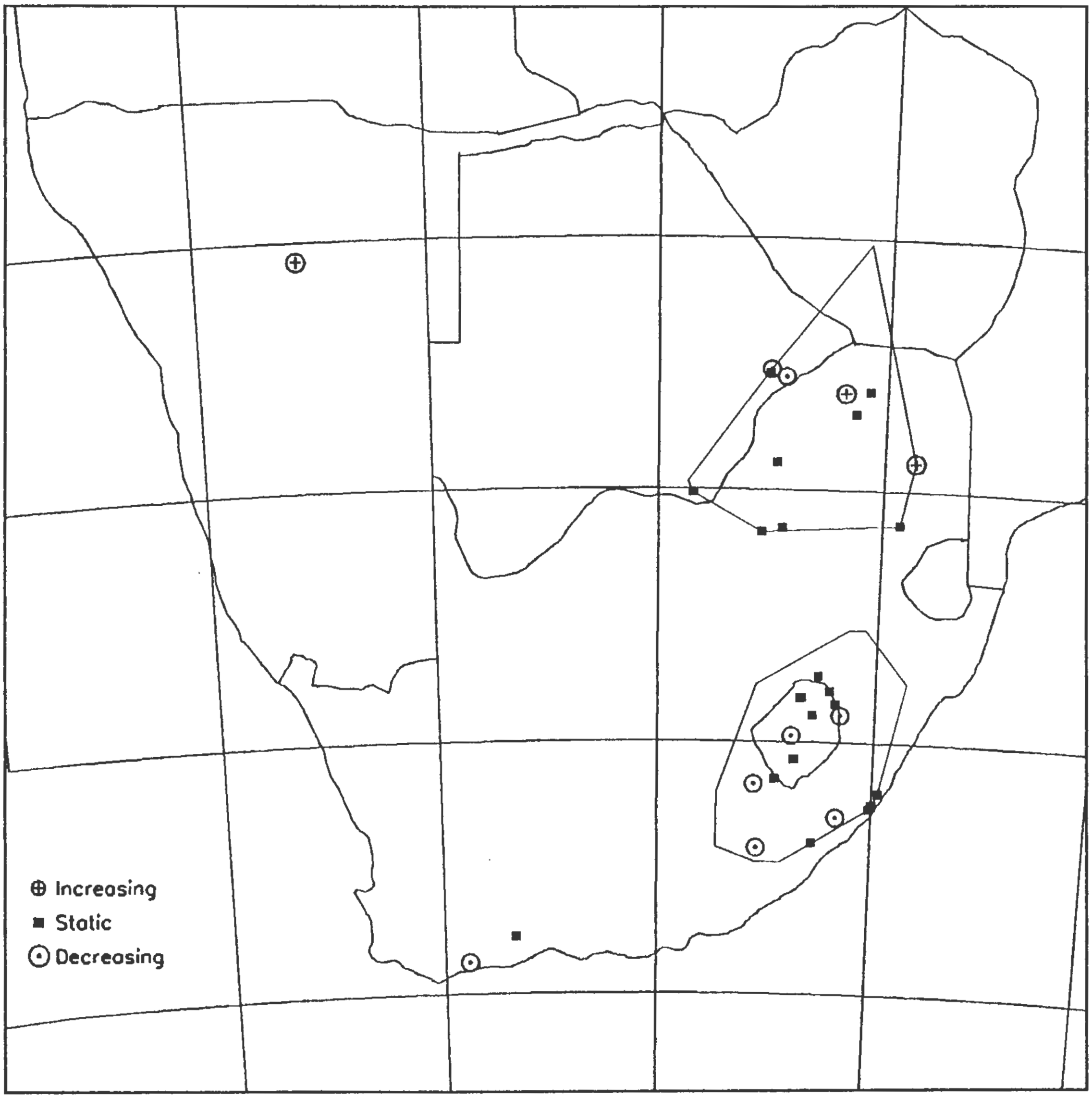


Figure 3.10 Spatial location of all active breeding colonies for which there is an assessment of change. Convex polygons enclose all active sites in two regions: a) Transvaal, Botswana and Zimbabwe and b) Natal, OFS, Transkei, Eastern Cape and Transkei.

Orange Free State Province

There are 27 sites in the Orange Free State (OFS), including Qwa Qwa, which have been considered breeding colonies or roosts of the Cape Vulture. All but two (i.e. 7.4% of 27) of these sites have been documented but only half of all sites are still active (Table 3.6). There is a wide range of dates at which sites were last documented; three sites (i.e. 11% of 27) are of unknown date, one (3.7%) was documented between 1951 and 1970, four (15%) from 1971 to 1975, eight (30%) between 1976 and 1980, seven (26%) from 1981 to 1985 and four (15%) post 1985. Of the 11 sites at which birds have bred three (i.e. 27% of 11) are now abandoned, one (9.1%) is rated as 'was a colony once', one (9.1%) is considered 'possibly a colony', and one (9.1%) is used sporadically. There are also three (27%) proven breeding colonies. Seven of the 21 (i.e. 33%) suspected roost-only sites are abandoned, four (19%) are used sporadically, seven (33%) are assessed as 'is a roost now' and the remaining three (14%) are active roosts.

There are only about 35 breeding pairs of Cape Vultures left in the OFS and these constitute 0.7% of the breeding population while there are just on 500 birds in the Province making up 4.1% of the total population. The active sites are all located along, or near the southern borders with Lesotho, Transkei and the Cape and along the eastern escarpment border with Natal. The Cape Vultures are confined to this belt because:

1) This is the small stock farming area.
2) The interior and north of the OFS are given over to dry-land crop farming.
3) These sites are within striking distance of the small stock farms in the adjacent regions (i.e. Natal, Lesotho, northern Cape and Transkei).

The sites are all small and act mainly as permanent, winter or sporadically-used roosts. It is likely that the O.F.S. never had many sites and that they were mainly on the periphery of the Province's southern and eastern borders. The ratio of breeding birds to all birds in the OFS is 12%, which is the lowest of any region and this indicates that the OFS is a non-breeding region (see Table 3.10 below and associated discussion) and a candidate 'nursery' area (see Chapter Six below).

Currently one roost (i.e. 25% of four) is increasing (Bloukrans), two (50%) are constant and one (25%) is decreasing. Of nine sites which are now, or were once, breeding colonies three (i.e. 33%) are abandoned, one (11%) 'was a colony once', one (11%) is 'possibly a colony now' and four (36%) are active. Of the 24 roost-only sites seven (i.e. 29%) have been abandoned. For those sites for which there are historical data it is obvious that they have undergone a serve decline since the turn of the century.

Table 3.6

Active Cape Vulture roosts and colonies in the Orange Free State.

Site	Name	Co-ords	No. birds	No. pairs	Last visit	Trnd pair	Site type	Assessment certainty
183	Bakerskop	28202904	50	0	1987	N/A	Roost	Moderate
13	Bloukrans	28512715	30	0	1988	N/A	Roost	Moderate
34	Claasenskop	28412740	12	0	1988	N/A	Roost	Low
185	Kerkenberg	28312908	5	0	1988	N/A	Roost	Low
181	Malima Farm	28322841	50	15	1983	?	Satellite	Low
40	Mara (584)	27462921	15	0	1988	N/A	Roost	Low
48	Memel	27452943	4	0	1988	N/A	Roost	Moderate
58	Nelson's Kop	28142927	132	0	1988	N/A	Roost	Moderate
184	Rensbergskop	28242917	40	0	1983	N/A	Roost	Low
182	Rondawelkop	28302842	5	0	1988	N/A	Roost	Moderate
180	Sentinal	28452849	50	19	1983	?	Satellite	Low
36	Witpunt 1100	28302857	4	0	1988	N/A	Roost	Low
66	Witsieshoek	28302847	50	1	1987	?	Satellite	Low
102	Zastron	30172704	55	0	1987	N/A	Roost	Moderate
		Ttals	502	35				

There are few Cape Vultures left in the OFS and it is my opinion that they are likely to get even fewer if the present rate of losses continue.

Transkei

There are 15 putative Cape Vulture sites for the Transkei and 14 of these have been documented, while nine are currently in use (Table 3.7). The Transkei sites are of recent documentation, eight (i.e. 53% of 15) sites have been documented since 1985, six (40%) sites were documented in the period 1981 to 1985 and two (13%) sites are of unknown date.

Of the ten possible breeding colonies, one (i.e. 10% of 10) is known to have been abandoned, one (10%) 'was a colony once', three (30%) are rated as 'possibly a colony', one (10%) is used sporadically thus leaving six, active, proven breeding colonies. There are eight sites which have no breeding component, one (i.e. 12% of 8) has been abandoned, one (12%) 'was a roost once', two (25%) are rated as 'possibly a roost', two (25%) are used sporadically thus giving two (25%) proven roost-only sites.

There are an estimated 545 breeding pairs in the Transkei and this represents 12% of the total breeding population while there are about 1265 Cape Vultures which constitute 11% of the whole population.

Table 3.7

Active Cape Vulture roosts and colonies in the Transkei.

Site	Name	Co-ords	No. birds	No. pairs	Last visit	Trnd pair	Site type	Assessment certainty
235	CalaMountain	31362743	30	0	1988	N/A	Roost	Low
348	Castle	30442828	30	10	1987	?	Nucleus	Moderate
18	Colleywobbles	32002837	800	350	1988	+/-	Nucleus	Moderate
349	ColonKoppe	30492821	60	30	1987	?	Nucleus	Moderate
35	Ku-Yeneni	31302910	25	10	1987	-	Satellite	Moderate
90	Mtentu	31143000	130	60	1987	+/-	Nucleus	Moderate
164	Mtzikaba	31182956	150	65	1987	+/-	Nucleus	Moderate
74	Ndakeni	30462906	30	15	1987	?	Satellite	Low
261	Vumenjani	32232752	10	5	1984	?	Satellite	Low
		Totals	1265	545				

The sites are located throughout the region. In terms of size, sites range from small to medium; and in terms of distance, they are in the spectrum of close to moderately far apart. The proportion of breeding birds is 78%, which is the second highest of all regions, indicating that this region is a 'breeding nucleus'.

There are no known major trends in numbers in the Transkei - all-in-all the region seems to be remarkably stable. Of four breeding colonies for which it is possible to provide an assessment of population trends, three are constant while one is decreasing. A similar pattern holds for the roost-only sites. Of ten breeding colonies seven (i.e. 70%) are active, one (10%) is rated as 'possibly a colony now', one (10%) 'was a colony once' and one (10%) has been abandoned. Of 13 roost-only sites nine (i.e. 69% of 13) are active, two (15%) are rated as 'possibly a roost now', one (7.7%) 'was a roost once' and one (7.7%) is abandoned

The Transkei, with Lesotho and the Natal Drakensberg, forms the second 'heartland' of the Cape Vulture with over a quarter of the breeding population. This area is important to the population as a whole as it has the lowest degree of human impact on Cape Vultures in the form of poisoning, persecution and disturbance (Piper, Mundy & Vernon in prep., see also Chapter Five below).

Transvaal Province

A total of 27 possible Cape Vulture sites have been proposed for the Transvaal, of these 25 have been documented but only half of these are still actively used (Table 3.8). For two sites (i.e. 8% of 25) there is no known date at which the site was last counted, one site (4%) was counted between 1971 and 1975, 12 sites (48%) were counted between 1976 and 1980 while the remaining 12 sites (48%) were counted during the years 1981 to 1985. During the period 1980 to 1984 Tarboton, Kemp & Kemp (1987: 42) adjudged there to be 12 breeding colonies in the Transvaal.

There are nineteen sites which are possible breeding colonies, two (i.e. 11% of 19) have been abandoned, two (11%) are rated as 'possibly a colony', six (32%) are rated as 'is a colony now', thus leaving eight active, proven breeding colonies. Of the ten roost-only sites, two have been abandoned, two are considered to be 'possibly a roost', one is used sporadically, four are rated as 'is a roost now' and three are rated as 'possibly a roost' and one roost is decreasing slowly. Thus it can be seen that status of the Transvaal roost-only sites is not well known.

The Transvaal holds over 2700 breeding pairs which constitute 61% of all breeding Cape Vultures while the total number of birds is at least 5900 representing 47% of the whole population. The number of breeding pairs was put at 1450 for the period 1975 to 1981 (Tarboton & Allan 1984) while the estimate was increased to 2500 to 3000 pairs for the period 1980 to 1984 (Tarboton, Kemp & Kemp 1987: 42) and later confirmed at about 3000 pairs breeding each year during the period 1980-1985, both years inclusive (Benson, Tarboton, Allan & Dobbs 1990: 134).

The possibility of colony switching between Nooitgedacht, Roberts' Farm and Skeerpoort and Kransberg and Groothoek needs to be documented and understood more fully. The major sites are distributed along the boundary between the highveld and western bushveld, the boundaries between the great escarpment and both the lowveld and western bushveld, and in the bushveld itself (Tarboton & Allan 1984). There are no active sites in the south-central grain farming and industrial region, nor are there any sites in the lowveld. All the breeding colonies occur on major cliffs, escarpments or mountains.

The sites are extremely large and spread out at great distances from one another. There are few non-breeding birds at the colonies and it can be hypothesized that there are likely to be almost no non-adult birds. The proportion of breeding birds is 94% which is the highest for all regions. However this ratio may be inflated as the number of non-breeding birds roosting at the major colonies is probably negatively biased (see above).

Table 3.8

Active Cape Vulture roosts and colonies in the Transvaal.

Site	Name	Co-ords	No. birds	No. pairs	Last visit	Trnd pair	Site type	Assessment certainty
12	Blouberg	23042904	1800	800	1985	+	Nucleus	Moderate
298	Glenfurnis Farm	23042858	35	10	1978	?	Satellite	Low
33	Groothoek	24282736	2000	1000	1985	+/-	Nucleus	Moderate
305	Loskop	23292919	50	10	1981	+/-	Satellite	Moderate
45	Manoutsa	24263040	1000	500	1983	+	Nucleus	Moderate
300	Mara, Zoutpansberg	23022936	175	55	1980	+/-	Nucleus	Moderate
61	Nooitgedacht	28522733	10	0	1983	N/A	Roost	Moderate
72	Roberts' Farm	25512718	350	145	1983	+/-	Nucleus	Moderate
306	Rooipoort	24122959	100	35	1981	N/A	Roost	Low
79	Skeerpoort	25452745	300	140	1983	+/-	Nucleus	Moderate
308	Uniondale	23002935	90	40	1983	?	Satellite	Low
311	Weltevreden	25403023	15	5	1981	+/-	Roost	Low
		Totals	5925	2740				

There are some interesting trends at some of the breeding colonies.

1) Some having declined and then recovered (these are Roberts' Farm and Skeerpoort, Verdoorn, Becker & Branfield 1992).
2) Some switching has taken place (the birds from Kransberg moved to Groothoek and the birds from Nooitgedacht moved to Roberts' Farm and back again 30 years later Verdoorn & Becker 1992).
3) Some colonies seem to be growing strongly (e.g. Blouberg and Manoutsa, see section 3.3 below).

There is enough historical data to provide an assessment of the rate of change in breeding numbers at eight breeding colonies. Two colonies (i.e. 25% of 8) are increasing, five (63%) are stable and one (13%) is decreasing. Of the 18 putative breeding colonies two (i.e. 11%) have been abandoned, two are rated as 'possibly a colony now' while 14 (78%) are active. Among the 24 roost-only sites there are two (i.e. 8.3% of 24) abandoned sites, four which are rated as 'possibly a roost now' and 18 (i.e. 75%) active sites.

The Transvaal, with Botswana, forms the core of the Cape Vulture population with about two-thirds of the entire breeding population. Some colonies are decreasing seriously while others are increasing. Because the region contains the bulk of the population it logical to assume that it should be subjected to a well-designed monitoring programme and that strong conservation measures should be taken to ensure the population does not decline as a result of human activities.

Zimbabwe

There is only one confirmed Cape Vulture site in Zimbabwe at Wabai Hill and its physical characteristics were adequately documented in the 1970's when it was also counted a number of times. However, there is only one casual record in the early 1980's. This site is no longer a breeding site, though it was once. The estimated 250 roosting birds in Zimbabwe comprise 2% of the total Cape Vulture population. Because of the number of birds it attracts and because of its position on the very edge of the species range it urgently needs to be monitored on an annual basis. Furthermore it is suspected that Wabai Hill acts as a 'nursery area' and so every attempt should be made to age the birds when the site is visited.

This site is in the south-central portion of the country. The number of birds roosting has shown considerable variation over the years, but the cause is not known. There is no evidence that birds are poisoned, disturbed or molested.

Birds are regularly recorded in the west of Zimbabwe at Hwange and Chizarira National Parks and in the south and they have been seen, sporadically, in the midlands (Mundy 1982).

Table 3.9
Active Cape Vulture roost in Zimbabwe.

Site	Name	Co-ords	No. birds	No. pairs	Last visit	Trnd pair	Site type	Assessment certainty
99	Wabai Hill	20072932	255	0	1983	N/A	Roost	Moderate

Summary

There are 441 putative Cape Vulture sites, of which 422 have been documented, spread over 11 of the 13 regions for which it has been reported (Table 3.10; Figure 3.6). Only 167 (42%) of these sites are currently active (Figure 3.7), half (84) only as roosts and half (83) as breeding colonies (Figures 3.3, 3.8 and 3.11). Is this an accurate reflection of the number of roosts and colonies? In my opinion the two regions which might yield more sites, after some concerted searching, are Lesotho and the Transkei. It is my opinion, from exploring the eastern sections of the Transkei, that there are a number of small sites still to be found and documented.

It should be noted that the numbers of birds and breeding pairs have been taken from reports submitted by many hundreds of observers and are thus unstandardized as to time of day, season of counting and counting procedure. This raises many problems which can not be dealt with here.

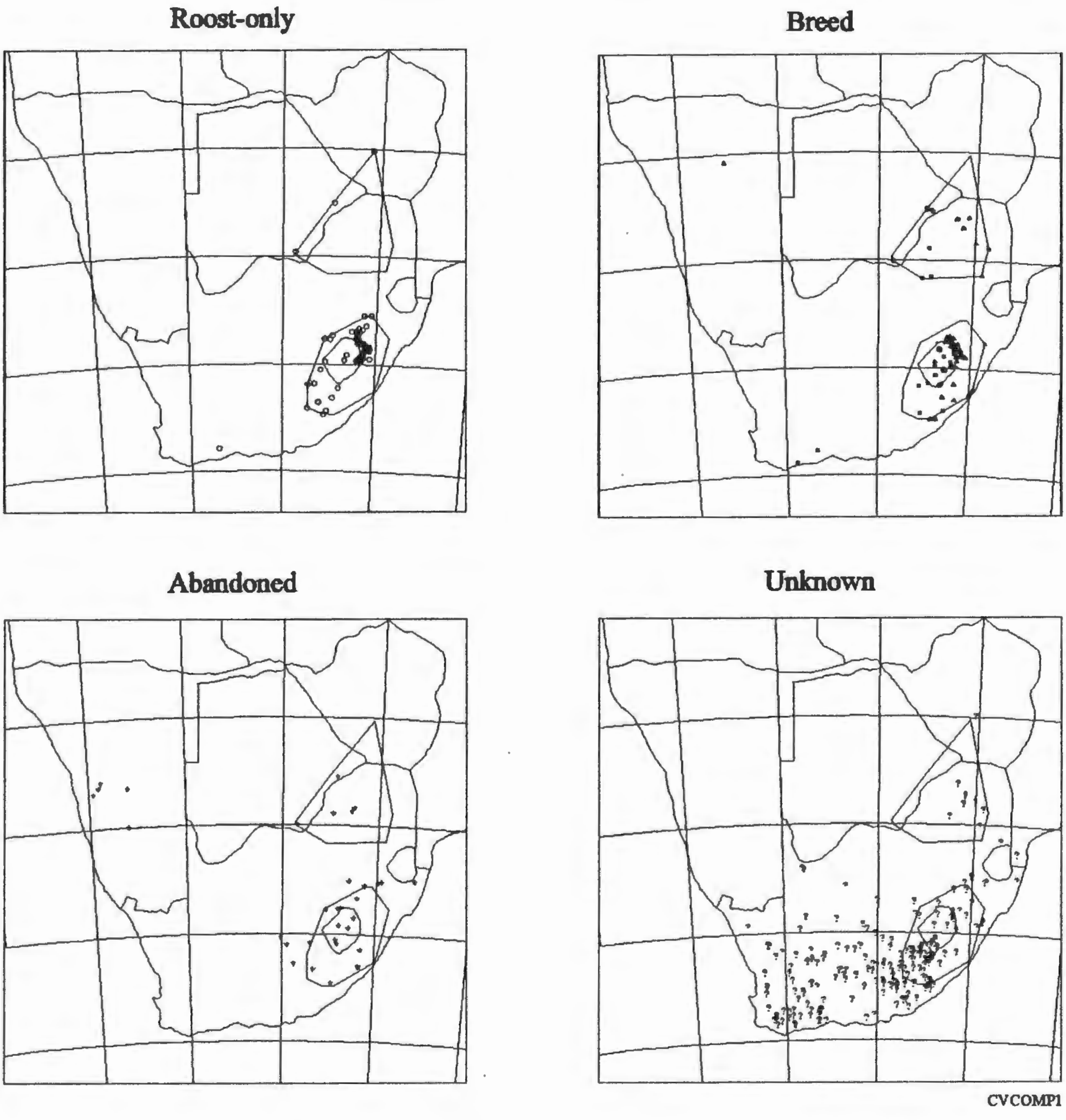


Figure 3.11 Comparison of the spatial location of roost-only, breeding and abandoned sites with sites of unknown status.

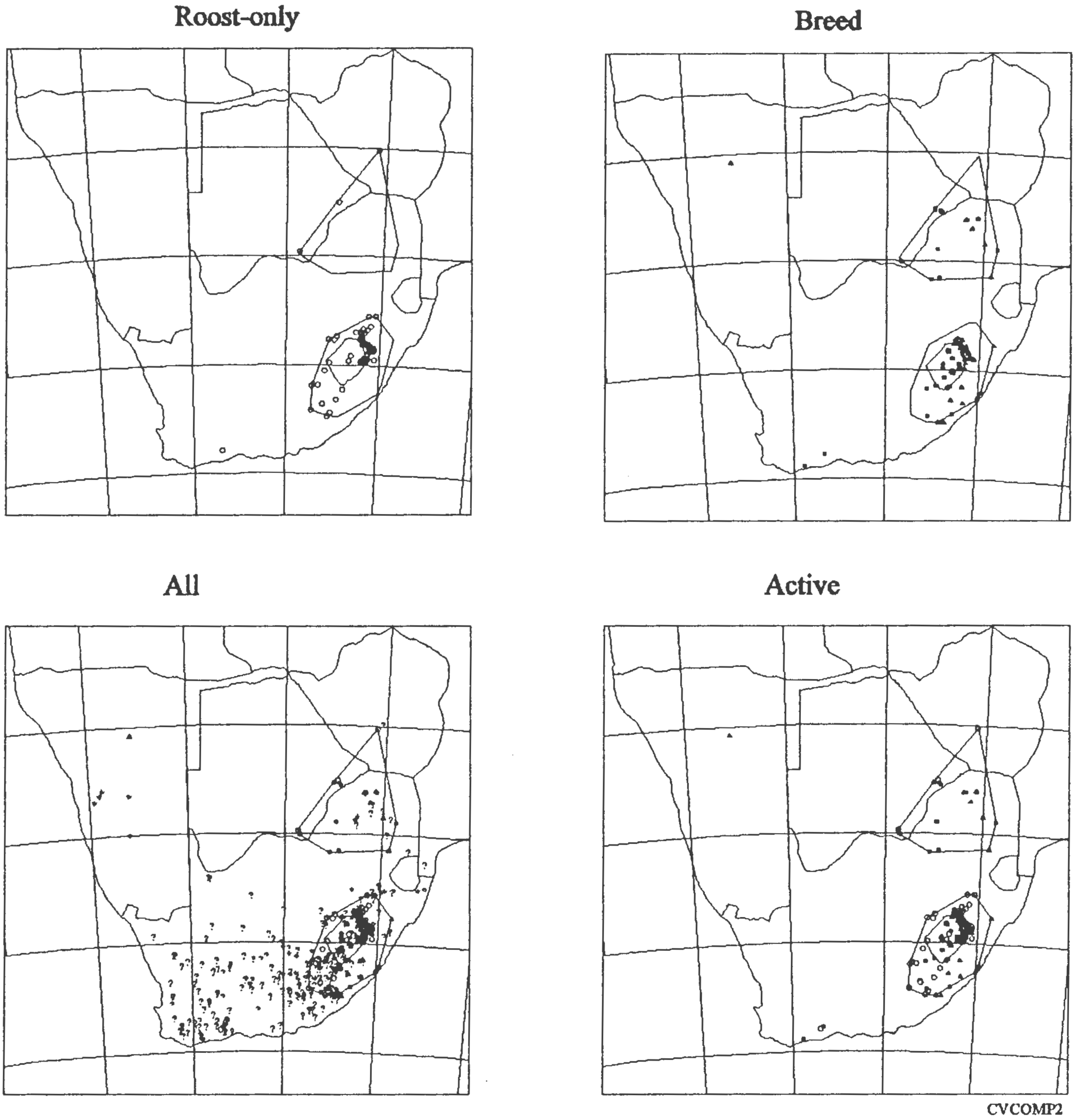
This species has suffer a contraction in range (compare Figures 3.6, 3.7 and); but not all putative sites are proven abandoned sites so this exaggerates the true contraction. The sites now cluster into two groups. The first is in the Transvaal and Botswana with two thirds of the Cape Vultures, and the second spans Lesotho, Transkei and the Natal Drakensberg. In addition, there are two isolated sub-populations located in Namibia and the southwestern Cape. To highlight these two groups a minimum convex polygon is shown around each (Figures 3.1 to 3.10)

Table 3.10

Summary of Cape Vulture sites and numbers.

Region	Active Roosts	Active Colonies	Active sites	Inactive Sites	Total Sites	Total birds	Total pairs	Proportion Breeding
Botswana	2	6	8	2	10	725	257	70.90%
Cape	10	5	15	175	190	552	109	39.49%
Lesotho	6	24	30	19	49	1228	457	74.43%
Mozambique	0	0	0	1	1	0	0	N/A
Namibia	0	1	1	6	7	18	5	55.56%
Natal	51	25	76	15	91	1518	267	35.18%
OFS	11	3	14	14	28	502	35	13.94%
Swaziland	0	0	0	1	1	0	0	N/A
Transkei	1	8	9	12	21	1265	545	86.17%
Transvaal	2	11	13	10	23	5925	2740	92.49%
Zimbabwe	1	0	1	0	1	255	0	0.00%
Totals	84	83	167	255	422	11988	4415	73.66%

The total Cape Vulture population is estimated at nearly 12 000 birds while the breeding population is just over 4400 pairs. What confidence can be placed in these figures? In the last decade there has been much interest in the Cape Vulture and at the same time there has been a massive bird-watching exercise co-ordinated by the Southern African Bird Atlas Project (SABAP; see section 3.2.5 below), and very few new breeding colonies have been located (Piper, Mundy & Vernon in prep.). Thus I an fairly confident that the total number of colonies is accurate, but I am less confident that the estimates of breeding pairs is as accurate. Not all the counts have been undertaken by competent observers and not all observers use the same methods and terminology, though a considerable effort has been put into homogenizing the estimates. It is certain that there is a negative bias in the counting of non-breeding birds. In some regions small roosts have certainly been overlooked (e.g. Transkei pers. obs.), in some regions only the colonies have been counted (e.g. Transvaal, Benson, Tarboton, Allan & Dobbs 1990), while in other regions the non-breeding birds have not been counted at all because they use electricity towers or trees for roosting (e.g. northern Cape and western Botswana; see Mundy 1983; Borello 1987). A better idea of this under-count will come from an examination of the SABAP data (see section 3.2.5 below).



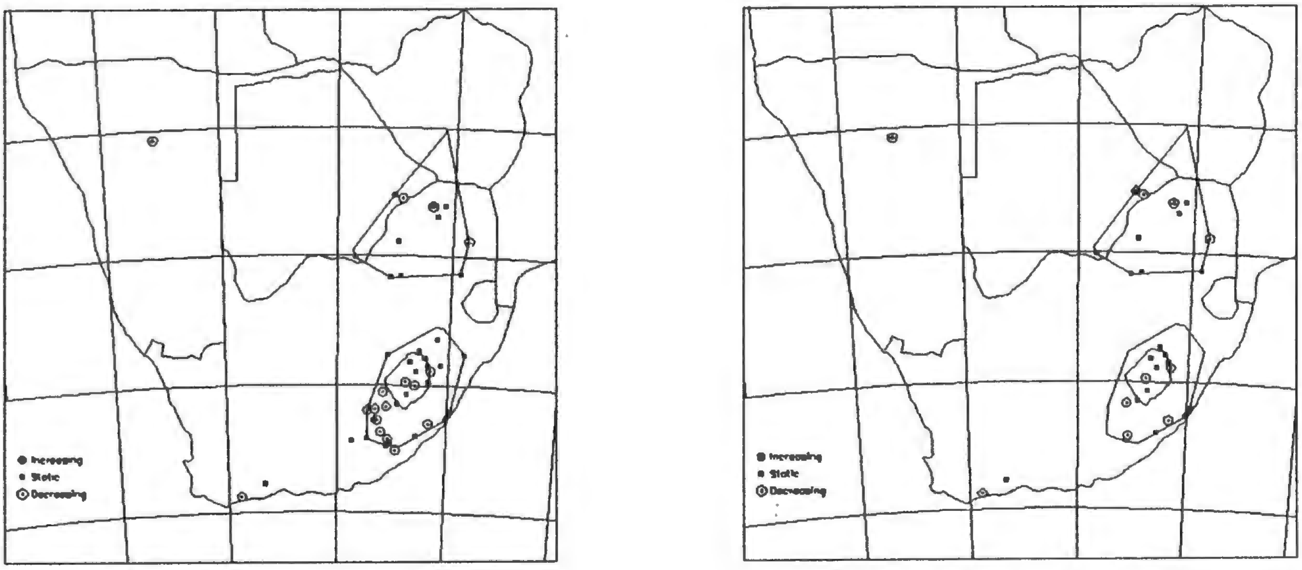
Roost-only

Breed

All

Active

Figure 3.12 Comparison of all putative sites with active, roost-only and breeding sites.



Changing Roosts

Changing colonies

Abandoned

Active

CVCOMP3

Figure 3.13 Comparison of all roost-only and breeding sites where rates-of-change of numbers are known with abandoned and active sites.

The proportion of breeding birds, for the whole population, is nearly 74% but it varies from 0% to 92.5% (Table 3.10) and it is likely that there is a positive bias in estimating this proportion, by varying amounts because of the reasons outlined in the previous paragraph (i.e. negative bias in estimating non-breeders). Later in this chapter independent estimates will be provided of age-ratios and will be used to test these arguments.

The 'age' or 'currency' of these data vary considerably from region to region (Table 3.11) with some regions having been assessed fairly recently (e.g. Lesotho, mostly post-1986) and others more than 15 years ago (e.g. Cape, mostly pre-1980). This is probably the most serious criticism of this data-set: it is not current. In some cases the data are to hand, but have not been entered into the Site Register (i.e. Piper, Mundy & Vernon in prep.), in others, the counts have been made but are yet to be analyzed and published. There is a serious need for monitoring to continue, at least at key sites, but these have yet to be identified. A set of recommendations is also needed for the frequency and protocols of counting Cape Vultures at roosts and colonies.

Natal is the region with the highest number of active sites, followed by Lesotho and the Cape (Figure 3.12), but these regions tend to have small sites and so they do not have the highest numbers of birds and breeding pairs. Most Cape Vultures are to be found in the Transvaal, with Natal and the Transkei taking second and third places, respectively. When looking at breeding pairs the order changes again to the Transvaal, Transkei at Lesotho. Looking at the proportion of breeding birds it may be seen that the Transvaal, Transkei, Lesotho and Botswana are 'breeding cores' (more than 70% breeding) while the other regions are non-breeding areas (<40% breeding), except for Namibia which consists of a small, single site and is a special case as an isolated remnant.

Table 3.11

Summary of year in which Cape Vulture sites were last visited.

Years Region	1971 -1975	1976 -1980	1981 -1985	1986 -1990	Total
Botswana	0	0	2	6	8
Cape	1	8	2	4	15
Lesotho	0	0	5	25	30
Namibia	0	0	0	1	1
Natal	0	0	73	3	76
OFS	0	0	3	11	14
Transkei	0	0	1	8	9
Transvaal	0	2	11	0	13
Zimbabwe	0	0	0	1	1
Totals	1	10	97	59	167

Table 3.12

Population trend of birds at active sites.

Region	Unknown	Increase slowly	Constant	Decrease slowly	Decrease rapidly	Total
Botswana	5	0	3	0	0	8
Cape	7	0	5	3	0	15
Lesotho	20	0	8	1	1	30
Namibia	0	1	0	0	0	1
Natal	73	0	3	0	0	76
OFS	11	0	2	1	0	14
Transkei	6	0	3	0	0	9
Transvaal	5	2	6	0	0	13
Zimbabwe	1	0	0	0	0	1
Totals	128	3	30	5	1	167

Most of the active sites were last visited in the early 1980s (Table 3.11), with about a third having been assessed in the last five years of the decade (though there are some sites which have not yet been updated on the Site Register). Assessments of population trends have been made for 39 roost-only sites (Table 3.12; Figures 3.9 and 3.13) of which three are increasing and six decreasing. The decreasing sites are mainly in the eastern Cape, Transkei and Lesotho while the increasing sites are in the Transvaal and Namibia.

For the 26 breeding colonies for which an assessment of population trends was possible three were found to be increasing and two are decreasing (Table 3.13; Figures 3.10 and 3.13); their spatial location is much the same as it is for active sites.

Table 3.13

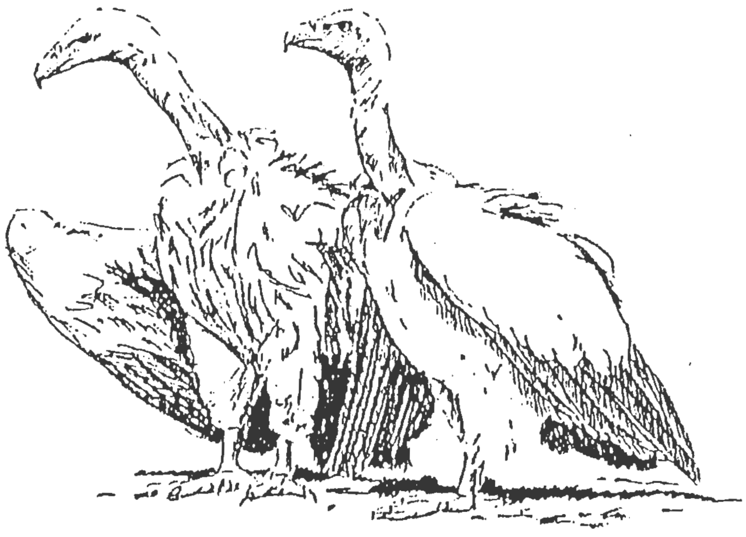
Population trend of breeding pairs at colonies.

Region	Unknown	Increase slowly	Constant	Decrease slowly	Decrease rapidly	Total
Botswana	4	0	2	0	0	6
Cape	2	0	2	1	0	5
Lesotho	16	0	7	0	1	24
Namibia	0	1	0	0	0	1
Natal	24	0	1	0	0	25
OFS	3	0	0	0	0	3
Transkei	5	0	3	0	0	8
Transvaal	3	2	6	0	0	11
Totals	57	3	21	1	1	83

There are a large number of sites which are not currently active (Figure 3.4) and these are, as expected, in the Cape, Lesotho, OFS and Namibia. But I am surprised to see how many there are in the south-central Transvaal; this region has possibly lost more sites than initially expected.

Notwithstanding the above caveats, I am confident that the Site Register data (i.e. Piper, Mundy & Vernon in prep.) have yielded a relatively accurate, if not absolute, picture of both the spatial distribution and numbers of Cape Vultures.

This section provides a summary of the numbers of Cape Vultures counted at colonies and roosts and give some idea of the spatial distribution of the population. In the next two sections attention is focused on estimating the proportion of adults (as a first step to a study of the age structure) and the breeding proportion of the population.



3.1.2 Age composition

In general terms, the age and sex composition of a population are a consequence of its age-specific survival and age-specific fecundity rates (Goodman 1967). For raptors, in particular, the ratio of young to adult has been investigated across a number of species (Amadon 1980). Thus a knowledge of age structure is of interest in its own right.

Lacking direct estimates of survival rates a number of authors have suggested using the proportion of birds in each age-class to make inferences about population dynamics (see summary of studies: Table 3.14). Thus it would seem that it would be of some value to collate the information available on Cape Vulture age-classes. However, the use of age-ratios to make inferences about population parameters should be used with caution (Grier 1979).

Various methods of ageing Cape Vultures have been proposed (e.g. Komen 1986; Mundy 1973; Piper, Mundy & Vernon 1989) which are mostly in agreement with one another. Ageing criteria have been used by a number of observers in the field to estimate the ages of individuals in groups of Cape Vultures (Table 3.15). Age composition can be seen to vary from region to region (Figure 3.14).

It has been shown for both Cape and African Whitebacked Vultures (Mundy 1982: 101, 248 & 262) that first year birds are driven away from their natal colonies because of their inability to compete with the more efficient adults. Consequent on this it has been suggested that the Cape Vulture population will be found to be spatially heterogeneous in terms of its age structure (Vernon & Robertson 1982). Thus it is to be expected that the proportion of non-adult birds should increase with distance from breeding colonies and this has been shown graphically (Richardson 1984:340). This hypothesis will be tested in section 3.1.3 below.

The age-ratio data (Table 3.15) are ordered from highest to lowest proportions of adults. Each site is labelled with the letter that appears on the accompanying map (Figure 3.14). The data are divided into four groups, with respect to age-structure: A, (B, C & D), E and F. The three samples B, C and D are homogeneous in terms of their age-structure (Chi-squared test, $p>0.1$); while each of the other groups differs significantly (Chi-squared test, $p<0.01$) from its neighbours.

Site A is close to two large Cape Vulture colonies (Skeerpoort and Roberts' Farm) with over 300 breeding pairs; sites B, C and D are at, or close, to small breeding colonies (probably <50 pairs) while sites E and F are far from the nearest breeding colonies. Dronfield Ranch at Kimberley is about 400 km from the breeding colonies in the Transvaal and Botswana (Mundy 1983) but is closer to the breeding colonies in Natal and Lesotho. It is likely that Mundy (1983) only considered the distances to the Transvaal and Botswana colonies because he saw ringed immatures from there.

It is seen from these data that the ratio of adults to immatures is high for those sites close to breeding colonies but low farther away. Thus, these results bear out the hypothesis of Vernon & Robertson (1982) and observations of Richardson (1984) who found that at about 40 km from the nearest breeding colonies the proportion of adults was 91%, at 75 to 125 km it was 68% and at 240 to 350 km it was 14%.

Table 3.14

Summary of studies advocating the use of age-structure to elucidate population parameters.

Species	Region	Period	Purpose	Authors
B/V	Ethiopia	1963-75	Survival	Brown (1977)
B/V & PN/V	East & West Africa	?	Ditto	Brown & Pomeroy (1984)
Brown Pelican	?	?	Monitor pop.	Schreiber & Schreiber (1983)
E/V	Cape Verde Islands	Early 1950s	?	Bourne (1955)
European Starlings	New Zealand	Late 1970s ?	Pop. dynamics	Flux & Flux (1981)
Mute Swan	Sweden	1972-86	Pop. maturation	Mathiasson (1987)
European Sparrowhawk	Britain	?	Survival	Newton, Marquiss & Rothery (1983)

Note: B/V = Bearded Vulture E/V = Egyptian Vulture, PN/V = Palmnut Vulture

Table 3.15

Observations of age-structure in the Cape Vulture.

Region	Period	Ratios First:Imm:Ad	Proportion of adults	Sample	Authors
A Spring Farm	1981-4	49:90:864	86%	1 003	Mundy, Ledger, Friedman & Butchart (1987)
B Giant's Castle	1983-4	4:8:43	78%	55	Barnard & Simmons (1985)
C Giant's Castle	1982	243:374:1459	70%	2 076	Brown (1987)
D Potberg	1981-2	(1st+Imm=17):40	70%	57	Robertson (1984)
E Zimbabwe	mid-1970s	(1st+Imm=17):10	37%	27	Ledger & Mundy (1975)
F Dronfield Ranch	mid-1970s	147:90:10	4%	247	Mundy (1983)

Note: the data of Richardson (1984) are not included here because data from different sites were lumped together, but see below for a summary of his results.

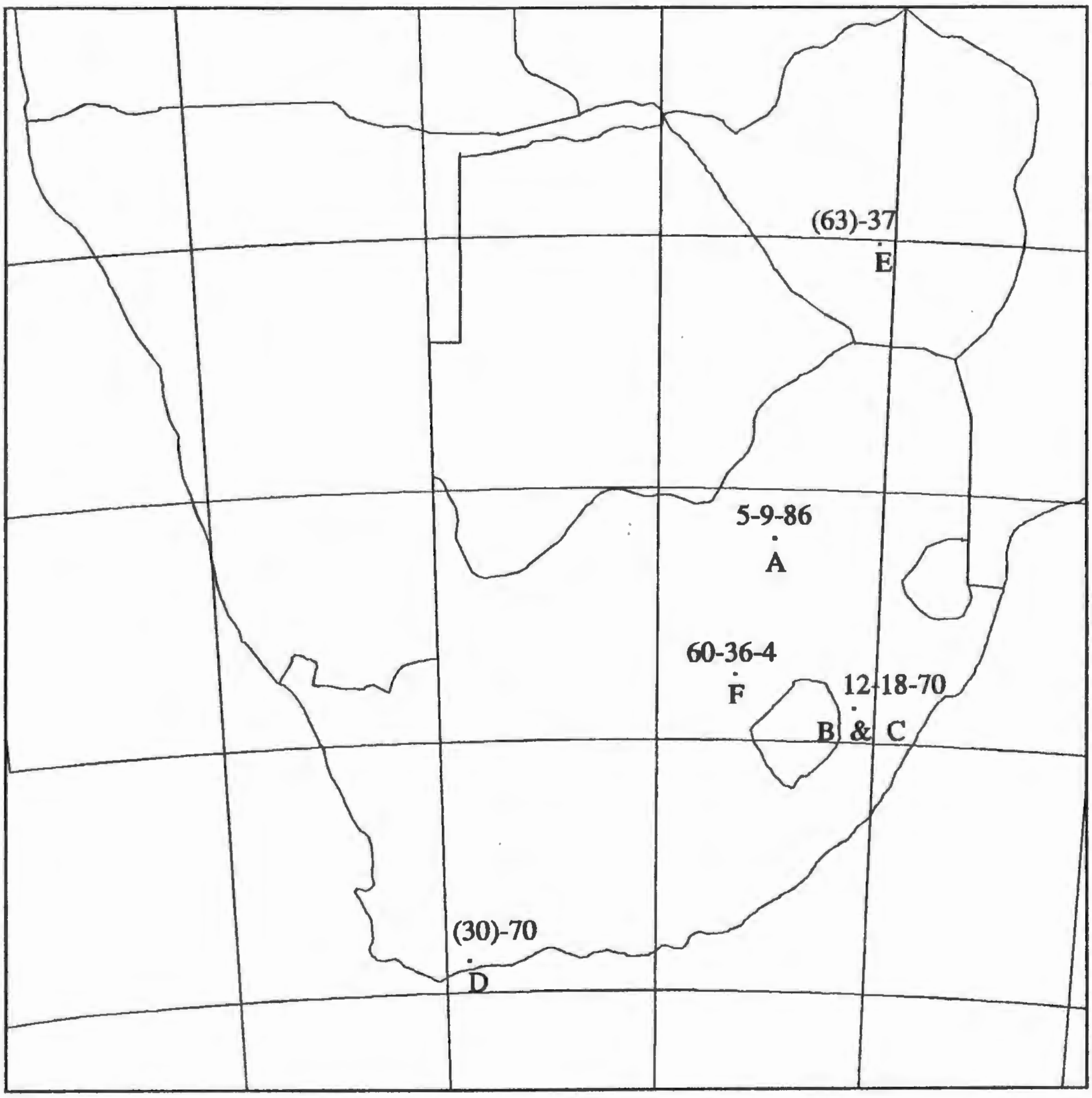


Figure 3.14. Spatial variation in the percentage of birds as First Years, Immatures and Adults. Where figures are given in parentheses they represent the percentage of First Years and Immatures grouped together. Letters refer to the spatial locations of Table 3.15.

3.1.3 Proportion of breeding birds

It is possible to estimate the proportion of breeding birds at a colony by counting the total number of birds roosting at the colony and by enumerating the number of active nests; this is best done at the start of the breeding season when most of the potential breeding pairs are present (see Chapter Four below). Unfortunately, this technique is likely to underestimate the number of non-breeding birds: they may not be tied to a particular roost or colony and they may just not return to a roost or colony every night. There are 167 active Cape Vulture sites of which 83 are breeding colonies (Table 3.10) and these vary dramatically in size (Figures 3.15 A & B respectively). Comparing the cumulative curves it is seen that the active sites' curve (i.e. A) initially rises faster than the colonies' curve (i.e. B) and this indicates that there are proportionately more smaller sites than colonies. This suggests that the colonies are not a random selection from all sites. In fact, it is noted that the larger breeding colonies tend to have a higher proportion of breeding birds (Figure 3.16).

This raises the question: 'Do the biggest breeding colonies attract more breeders and consequently exclude birds not breeding?' The relationship between the proportion of breeding birds, p at a colony of B birds can be formulated as a binomial model.

Binomial $(b,B;p) = f(B)$

Where

p = proportion breeding
B = No. of birds
b = No. of breeding birds.

To test whether the proportion of breeding birds, p is independent of the total number of birds, B it is tempting to plot p against B (Figure 3.16) and fit a linear regression. This cannot be done because the distribution of p is not normal (except for large samples), is bounded ($0 \leq p \leq 1$) and not symmetric (except for $p = ½$). Various transformations have been suggested (e.g. arc sin, McCullagh & Nelder 1989: 105 ff.) but now days these are eschewed in favour of the generalized linear model (GLM; loc. cit.: 98 ff.). The GLM uses the logit transform as its link function.

$\text{Logit}(p) = \text{Ln}(p/\{1-p\})$.

A linear model can be constructed with the number of birds, B as the independent variable.

$\text{Logit}(p) = \alpha + \beta * B$

The GLM can be fitted using the MODEL and FIT routines of GENSTAT-5 package (Anon. 1988: 347 ff.) and this provides a fit which is 'exact' in a maximum likelihood sense.

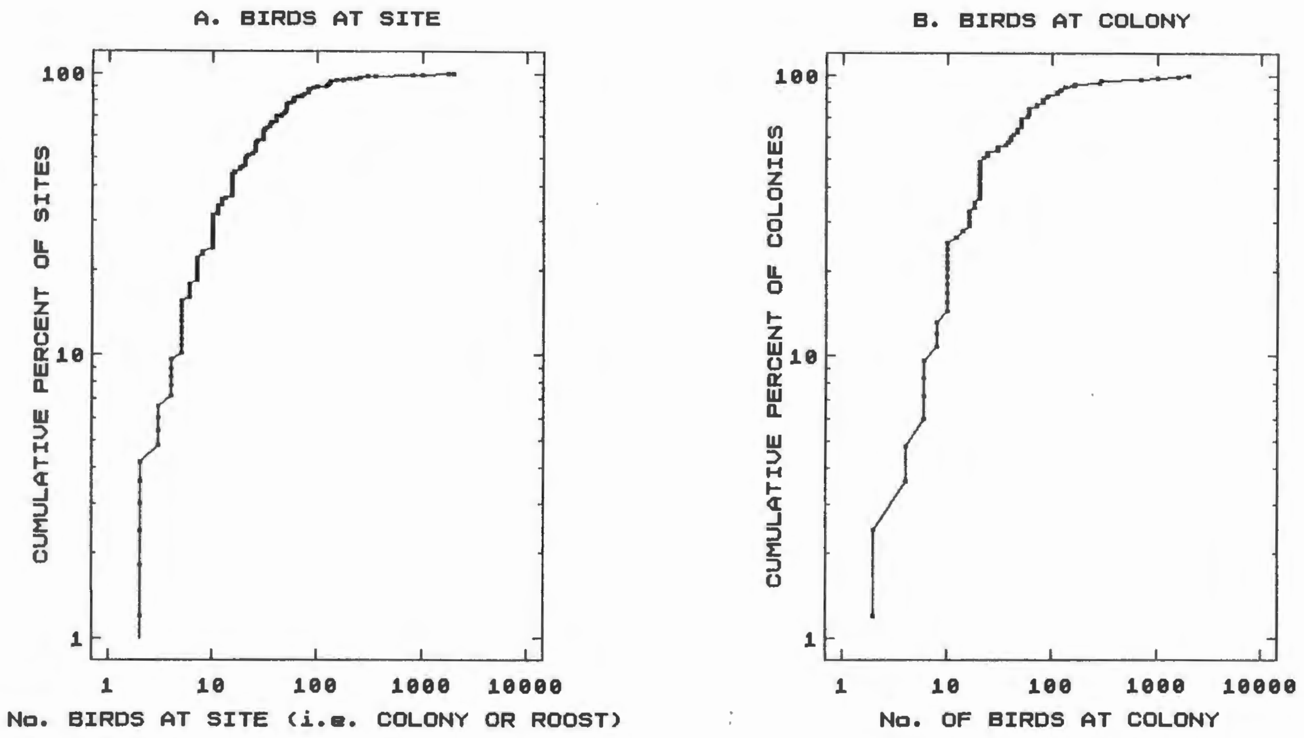


Figure 3.15 A. Cumulative percentage of sites plotted against the number of birds at a site (N=167). B. Cumulative percentage of colonies plotted against the number of birds at a colony (N=83).

If the proportion of breeding birds, p is independent of the number of birds at the site, B then Logit(p) will also be independent of B, i.e. Logit(p) = α will be an adequate model. This one-parameter model (i.e. the null model) was rejected in favour of the linear model (reduction in deviance = 990 which is asymptotically chi-square, 1 df, $p << 0.01$). The parameters of the linear model are:

$\alpha = 0.8873$ (s.e.= 0.0351, $p<0.001$)
$\beta = 0.0012992$ (s.e.=0.0000497, $p<0.001$)

The predictor for the proportion, p is given as:

$$p = EXP(\alpha+\beta*B)/\{1+EXP(\alpha+\beta*B)\}$$

This GLM model may be compared with the raw data (Figure 3.16). In order to see the maximum variation in the data, both p and B are plotted on logarithmic scales along with the logit regression (Figure 3.16); note that on log-log axes the best-fit GLM is not linear (plotting Logit(p) vs B yields a linear regression but, in my opinion, it is not easy interpret the Logit function). For sites of 10, 100 and 1000 birds the predicted proportions of breeding birds, from the linear model, are 71.1%, 73.4% and 89.9% respectively.

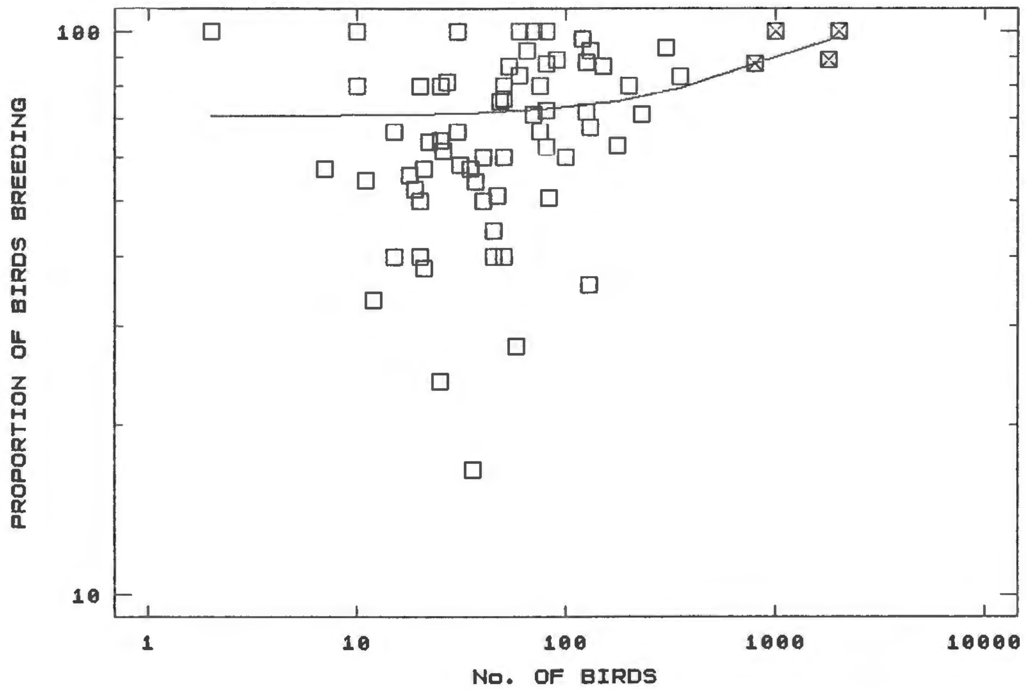
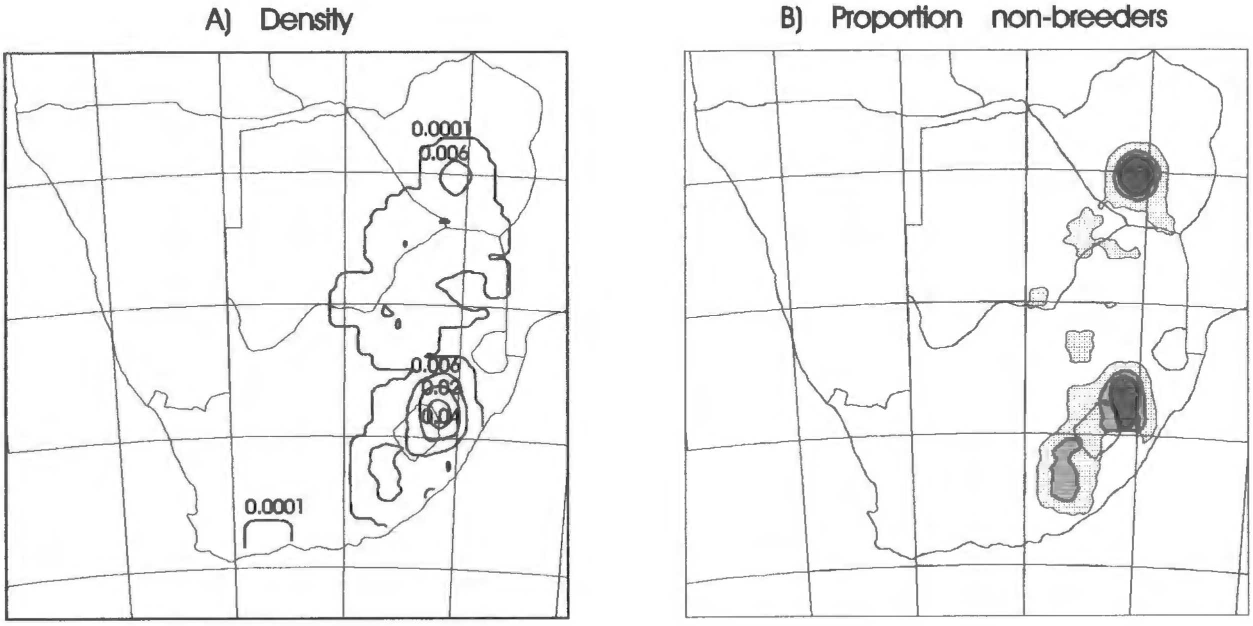


Figure 3.16 Variation in the proportion of birds breeding at a site with the number of birds at the site. The logit regression has been fitted using GLM.

The last four points in the regression (i.e. the largest colonies with approximately 800, 1000, 1 800 and 2 000 birds, respectively and shown as crossed out points on Figure 3.16) all have high leverages (see Cook & Weisberg 1982), i.e. they have an inordinately large influence on the parameters of the regression. Removing them actually increases the slope of the regression (from 0.0012992 to 0.003759, $p< <0.001$). In addition, 38 of the 83 data points have large residuals. The goodness-of-fit of the regression may be measured by the residual deviance ($=1473$) which is distributed approximately as chi-square with 81 degrees of freedom, hence $p< <0.001$. This indicates that although there is a strong trend there is still much variation about it and the model is not an adequate explanation on its own.

There are two different explanations for this relationship, i.e. larger colonies have higher proportions of breeding birds. A high concentration of breeding birds may create an environment which is too competitive for non-breeding and immature birds (Mundy 1982: 101). However, I am inclined to the view that the number of non-breeders has not been adequately counted at the larger colonies; this is a direct consequence of the photographic technique used to count the large Transvaal colonies (Benson, Tarboton, Allan & Dobbs 1990; Tarboton, Allan & Benson 1984 and Tarboton, Allan & Benson 1987). The team lead by Benson and Tarboton also used ground-based counts but only to validate the nest censuses, not to count the non-breeding segment of the population. A count representing too high a proportion of breeding birds may be diagnostic of a poor counting technique.


A) Density

B) Proportion non-breeders

Figure 3.17 Spatial distribution of the non-breeding segment of the population. A. Population density as birds/km^2. B. Proportion of population not breeding - the three stippled zones are at 10%, 30% and 50%.

Given that the total number of breeding pairs is known then an estimate of the proportion of breeding birds at each colony is of no great interest, in itself. What is much more important, rather, is some indication of how this proportion varies geographically.

A method is proposed for constructing a map of the non-breeding segment of the population and its variation across the subcontinent. The Site Register data will be used later (see section 3.2.1 below for rationale and methods) to construct maps of the population density of both breeding and non-breeding birds. This is to be done using a variety of interpolation techniques which gives the projected total number of birds, $B_{(i,j)}$ and breeding pairs, $P_{(i,j)}$ on a uniform grid $_{(i,j)}$. Given that there are two birds to a pair then the number, $N_{(i,j)}$ and relative proportion of non-breeders, $R_{(i,j)}$ will be $\{B_{(i,j)}-2*P_{(i,j)}\}$ (Figure 3.17 A) and $N_{(i,j)}/B_{(i,j)}$ (Figure 3.17 B) respectively.

Using these maps the following interesting features are noted.

1) There are concentrations of non-breeders (measured as birds/km^2) in A) Zimbabwe, B) the eastern Cape and C) Natal and Lesotho along the Drakensberg range.

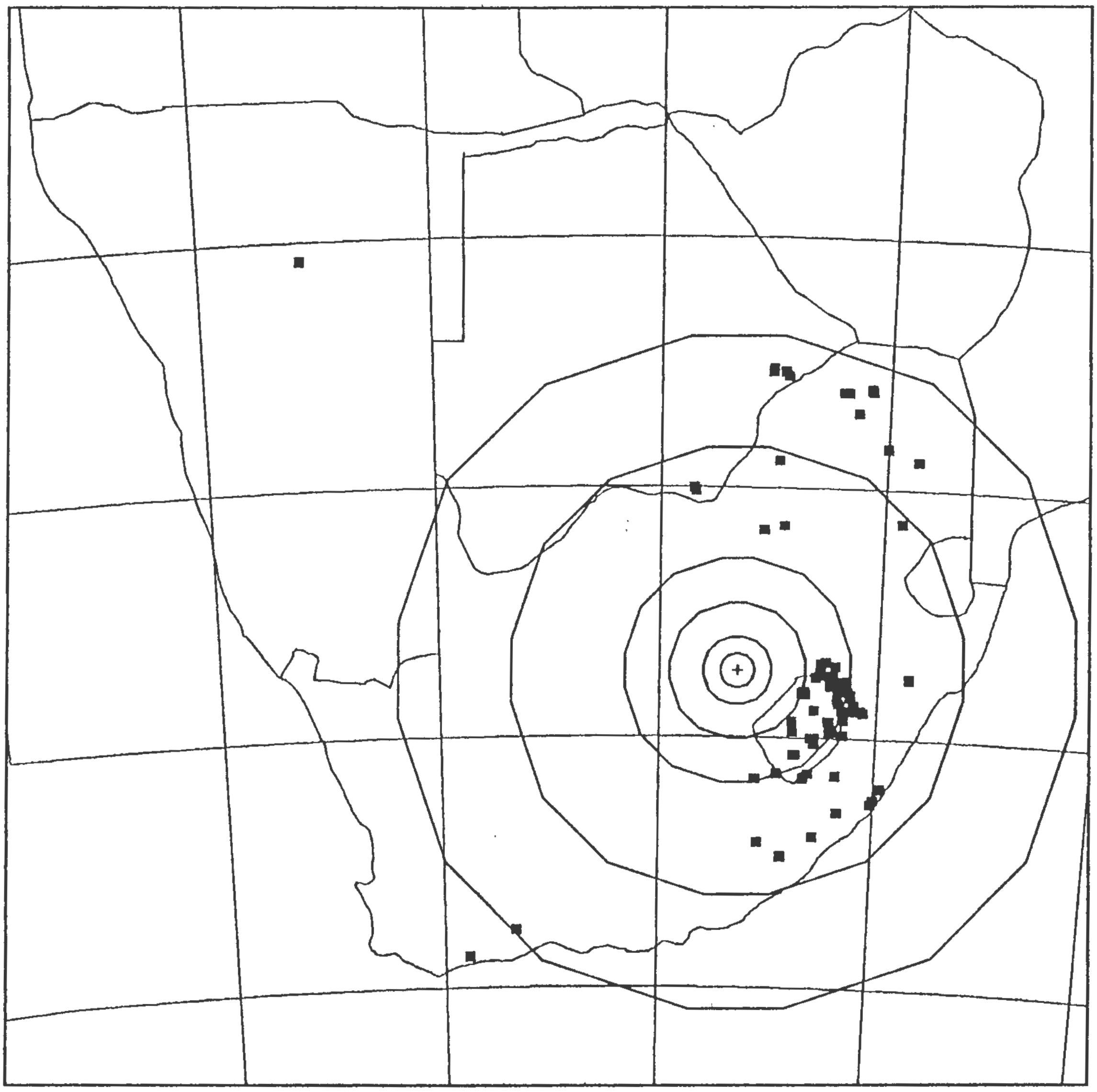


Figure 3.18 Computation of the ratio of breeding to total birds, S(x) as a function of distance from Dronfield Ranch. Circles are centered on Dronfield and are of radius 75,150, 300, 500, 1000 and 1500 km respectively. A samples of active sites (i.e. roosts and colonies) is shown.

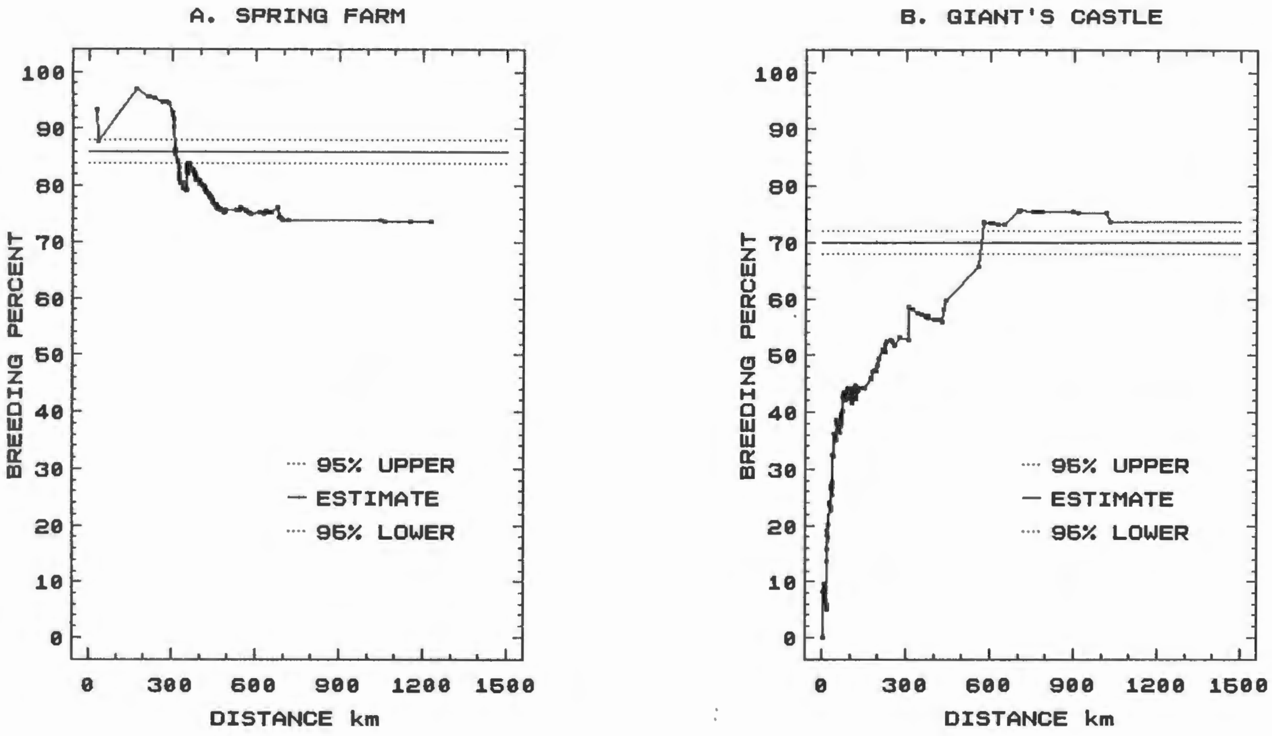


Figure 3.19 Breeding proportion as a function of distance from the locality at which the age-ratio count was made. A. Spring Farm. B. Giant's Castle.

2) The highest concentrations of non-breeders are in Zimbabwe and along the Natal-Lesotho Drakensberg.
3) The highest proportions of non-breeders, as opposed to the highest numbers of non-breeders, are in A) Zimbabwe, B) Natal and Orange Free State C) the eastern Cape, 4) northern Cape and E) Botswana (Figure 3.17 B).

These interesting distributions call for an explanation. Without offering any substantiating evidence, or motivation at this stage, it is suggested that the following factor is likely to be important in explaining the segregation of non-breeders from breeders. The areas of high non-breeding proportions are probably 'nursery areas', i.e. areas to which non-breeding birds go to avoid competition from adults who are more efficient foragers. If this is indeed true then these areas of high numbers of non-breeders are where there should be the highest numbers of recoveries of young birds (see Chapter Five).

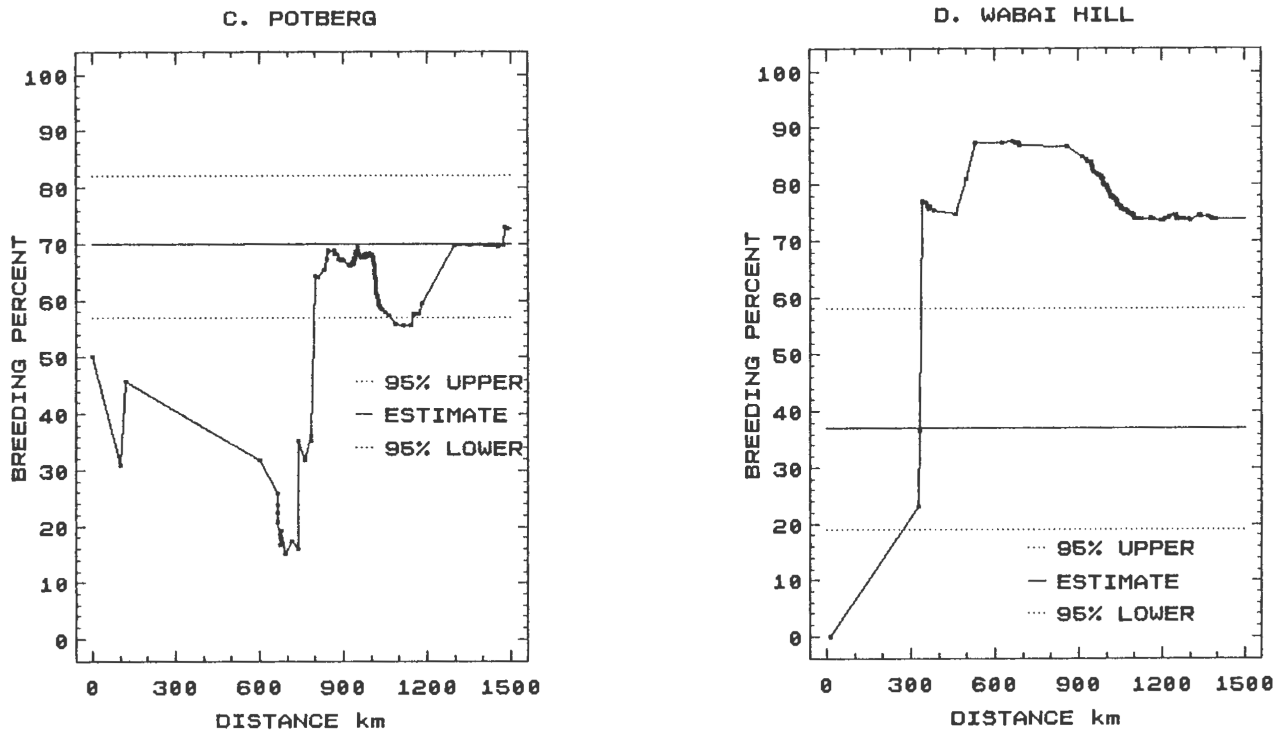
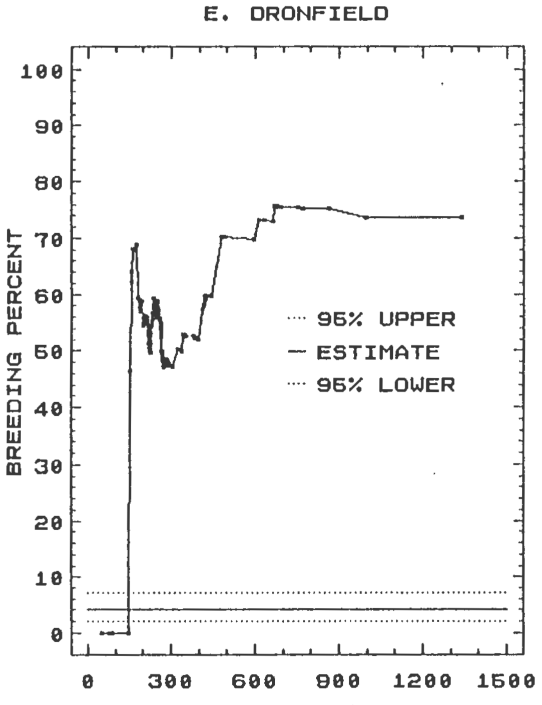


Figure 3.19 Breeding proportion as a function of distance from the locality at which the age-ratio count was made. C. Potberg. D. Wabai Hill.

These data may be checked, for veracity, against the age-ratio counts presented in the previous section (i.e. 3.1.2). To do this means making assumptions about the age at first breeding, i.e. assuming that few birds start to breed before they achieve adult plumage. But note that the proportion of breeding birds is not the same as the proportion of adult birds (see previous section 3.1.2) because 1) some birds can, and do breed while still in pre-adult plumage and 2) not all adults attempt to breed in every year (see Chapter Four below).

Age-composition data were presented for six samples at five sites (see section 3.1.2 above). These may be compared with the proportion of breeding birds in the surrounding region. The first way in which this may be done is as follows. Taking the point at which the age-composition estimate was made (e.g. Dronfield Ranch; Figure 3.18) a circle of radius x km is drawn and all the breeding pairs, P(x) and birds, B(x) within that circle are counted. From these two sums the proportion of breeding birds within a radius x, i.e. $S(x) = P(x)/B(x)$ may be computed. By plotting S(x) against x it is possible to compare the proportion of adults (from 3.1.2 above) with the proportion of breeders. Each of the six samples is now examined relative to its S(x).



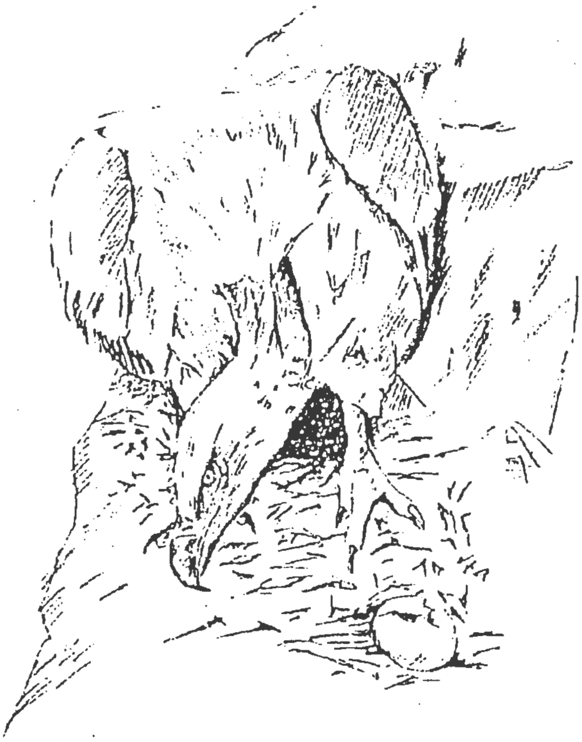


Figure 3.19 Breeding proportion as a function of distance from the locality at which the age-ratio count was made. E. Dronfield Ranch.

A) Spring Farm. With 864 adults out of a sample of 1 003, p=86% with 95% confidence limits of 84-88% (Diem & Lentner 1970: 85 ff.; all binomial confidence limits are computed using this set of tables). This is slightly lower than the nearby population (Figure 3.19 A).

B) Giants' Castle; Barnard & Simmons (1985). There were 43 adults of 55 birds aged, p=71%, 95% confidence limits are 65-88% (Figure 3.19 B).

C) Giants' Castle; Brown (1987). A much larger sample of 1 459 adults of 2 076; p=70% and 95% confidence limits are 68-72%. Both this, and the previous sample, yield values of the breeding proportion which are so much greater than that estimated (Figure 3.19 B) as to give cause for concern.

D) Potberg. The proportion is 70% (confidence limits 57-82%) based on a sample size of 57 and the proportion is slightly greater than expected (Figure 3.19 C).

E) Zimbabwe. This small sample of 27 birds had 10 adults, p = 37%, 95% confidence limits are 19-58% and are compatible with the estimated S(x), (Figure 3.19 D) but implying that the birds come from far away.

F) Dronfield Ranch. This site has the lowest proportion of adults (10 of 247) giving p = 4% and confidence limits of 2-7%. A comparison of this ratio with the appropriate S(x) (Figure 3.19 E) shows that these birds must come from far afield, see comments in Mundy (1983).

Table 3.16
Comparison of observed proportion birds in adult plumage with estimated proportion of birds breeding.

	Estimates of proportion breeding		
Region	Observed	From Figure 3.17 B	From radial function S(75)
Spring Farm	86%	48%	88% to 97%
Giant's Castle	78%	31%	43%
	70%		
Potberg	70%	33%	31% to 50%
Zimbabwe	37%	0.25%	0 to 23%
Dronfield	4%	24%	0%

A second method of estimating the proportion of breeding birds at a geographical location is to take the contour map of 'proportion of non-breeders' (Figure 3.17 B) and interpolate values at the points at which counts were made. These data are compared with the observed age-ratios and the estimated proportion of breeding birds within a radius of 75 km, i.e. S(75) (Table 3.16). A radius of 75 km is chosen because that is reckoned to be easily within a day's range (see arguments in section 3.2.1 below).

The three counts at Spring Farm and Giant's Castle come from observations at vulture restaurants and were probably made during the breeding season. As such it is to be expected that adults will dominate immatures and this may be the reason for the higher-than-expected proportion of breeders. On the other hand, during the breeding season one half of the breeding adults will be tied to the nest and so will be unavailable to be counted. This makes the ratios at Spring Farm and Giant's Castle even more biased in favour of adults. The high number of adults counted in Zimbabwe, far from any breeding colony is indicative of the large number of adults which do not breed and are thus not tied to any colony and so are free to wander.

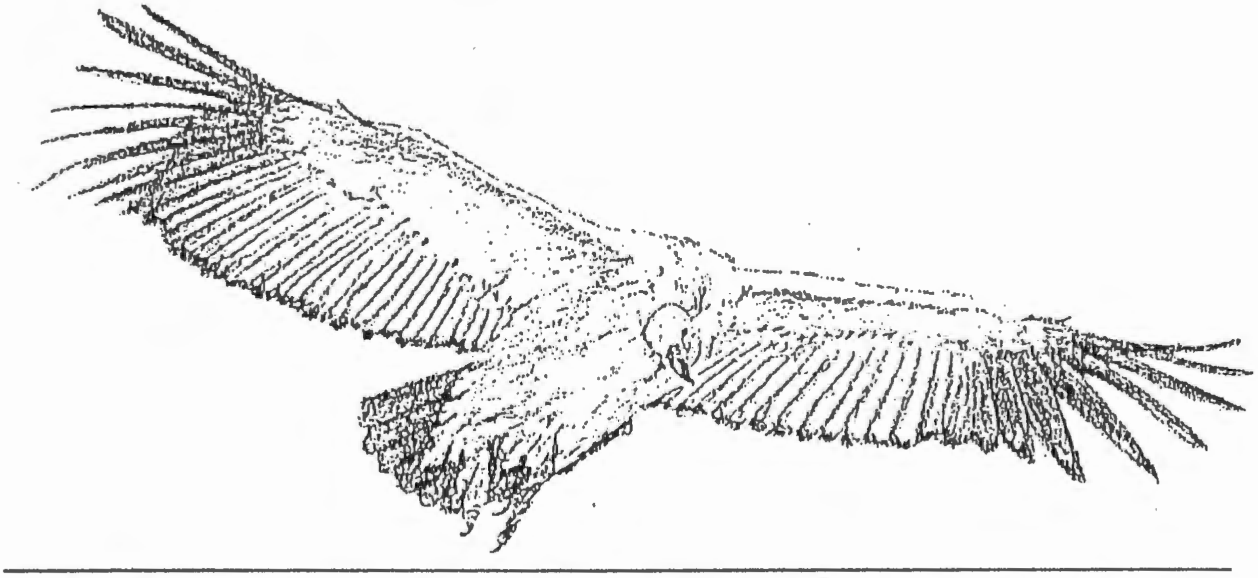
This analysis shows that the population's age-structure varies in space and is more complex than initially imagined. It is also important to consider how biased are the sampling techniques: counts at carcasses, roosts, colonies and along power-lines; for each of these are different methods of getting estimates of population structure. Each will have its own biases.

3.2 Distribution

With the exception of the maps in Mundy (1982) and Brooke (1984) all the Cape Vulture distribution maps published to date are no more than broad brush-stroke generalizations of anecdotal accounts of this species' dispersion (e.g. Maclean 1985; Steyn 1982)[1]. In fact, some of these maps show Cape Vultures in regions from which there have never ever been any records. Most Cape Vulture maps have been drawn at a scale of 1 in 45 000 000, or smaller, i.e. a 1 mm pencil thickness is 45 km on the ground. The time is now ripe for the construction of a set of maps which represent, with some spatial accuracy, the modern distribution of the Cape Vulture.

This modern Cape Vulture distribution will be elucidated from two data-sets: the Site Register (Piper, Mundy & Vernon in prep. and section 3.1.1 above) and the Southern African Bird Atlas Project (SABAP). The Site Register data give the approximate numbers of breeders at colonies and non-breeders at roosts, and using a variety of modelling techniques, these may be extrapolated as density maps. The distributional data come as sightings of Cape Vultures on bird species' check-lists submitted to the SABAP at the University of Cape Town. This latter data-set gives a spatial distribution which is in the form of an uncalibrated index; the challenge is to give this index meaning.

These new data-sets will enable maps to be generated which give a spatially accurate picture of how many Cape Vultures are where, and how many of them are breeders. This forms the basis of the spatial population models to follow.



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[1] The maps in Mundy, Butchart, Ledger & Piper (1992: 72, 77) are not discussed here because they are based, in part, on these researches.

3.2.1 Point spread models applied to the Site Register data

The data in the Site Register (Piper, Mundy & Vernon in prep.; section 3.1.1 above) give the numbers of Cape Vultures 'over-nighting' at roosts or breeding at colonies. There are a finite number of active Cape Vulture sites (167: 83 colonies and 84 roosts; Table 3.10) dotted over the southern Africa landscape. But these point densities do not show where a Cape Vulture might appear in its daily travels whilst foraging. To know where Cape Vultures wander and forage each day may not seem relevant to modelling their population dynamics, but it is important to know this for the following reasons:

1) It is necessary to have an 'average density map' for the Cape Vulture from the Site Register data so as to be able to compare densities with the SABAP sightings' data. This comparison is important because it may give insight into colonies or roosts which have been overlooked. Also, it may show where Cape Vultures are residing in areas far away from their 'traditional sites' ('traditional', that is, to us what studies them!). This is seen, most clearly, in the Cape Vulture sightings map for Botswana (Borello 1987), wherein it is shown that Cape Vultures have been sighted many hundred kilometres to the west, and northwest of the nearest known roost or colony.
2) A comparison of the SABAP sightings map with the 'average density map' from the Site Register may show which habitats are avoided by the Cape Vulture, e.g. open water and commercial plantations. This latter land-cover type is bound to increase steadily over the next 25 years and so may remove foraging zones from the Cape Vulture and cause declines in local populations and may also cause range contractions.
3) The foraging range of Cape Vultures is the primary link between its population dynamics and its food base; it would be most surprising if this species was not limited by food ('normally nest-sites and food govern the distribution of breeding raptors' Newton 1979: 54). An understanding of this linkage may be central to understanding the population dynamics of this species.

Density distributions

How does a typical Cape Vulture spread itself, so to speak, over its entire foraging zone, or home range, while based at a single home-site (i.e. roost or colony); averaged over time? Let the probability density distribution of its average density be $g(x,y)$. Based on common sense the following simple restrictions can be placed on $g(x,y)$:

1) The density can never be negative, i.e. $g(x,y) \geq 0$.
2) When integrated over the whole plane the sum of the densities must be 1.
3) There should be a finite, upper limit to $g(x,y)$, i.e. density should not tend to infinity anywhere; even at the home-site (i.e. roost or colony) which is where the maximum density will occur.

Naturally, in the real world, $g(x,y)$ will be a function of season, it will vary between good and bad years and will be different for birds of varying degrees of foraging competence. But, to start with, these models will be simplified by adding the following assumptions:

4) The distribution, in uniform countryside, may be radially symmetric; i.e. $f(r)=g(x,y)$, a function of only the radial distance, $r=(x^2+y^2)^{1/2}$ from the home-site which is assumed to be at the origin (0,0).
5) The average density, $f(r)$ is independent of the number of birds at the site.
6) All sites have the same density function, $f(r)$.

What reasonable functional forms can be motivated for the radial density function, $f(r)$? The following forms are suggested:

1) A uniform disc:

$$f(r) = \begin{cases} \alpha & \text{for } r \leq R. \text{ R is the maximum foraging range.} \\ 0 & \text{otherwise} \end{cases}$$

This model is too simple as it implies that vultures spend equal amounts of time in every portion of their range, even the most distant parts. However, it does provide a simple starting point for modelling dispersion and density.

2) Radial search model. If vultures choose a search direction, at random, at the start of each day's foraging and then fly outwards at constant velocity, v then they will all be at a radial distance, $r=v^*t$ after time t. Hence their density will be proportional to $1/r$:

$f(r) = \alpha/r$. Where α is a suitable constant.

3) Gravitational model. Arguing as for the previous model, but assuming that the further a vulture is from its home-site the less likely it is to wander away leads to the suggestion that the density could behave like the gravitational model:

$f(r) = \alpha/r^2$. Where α is a suitable constant.

4) Generalized, 'proper' inverse power models. Both models 2) and 3) above are 'improper', i.e. unbounded, in that $f(r)\to\infty$ as $r\to 0$. These models can be made 'proper', i.e. finite at $f(0)$, by incorporating an arbitrary offset (W. Zucchini and H. van Gysen pers. comm.). Furthermore they can be combined into a single inverse power model of the form:

$f(r) = \alpha/(r^{\beta}+\delta)^{\tau}$. Where α, β, δ and τ are suitable constants >0

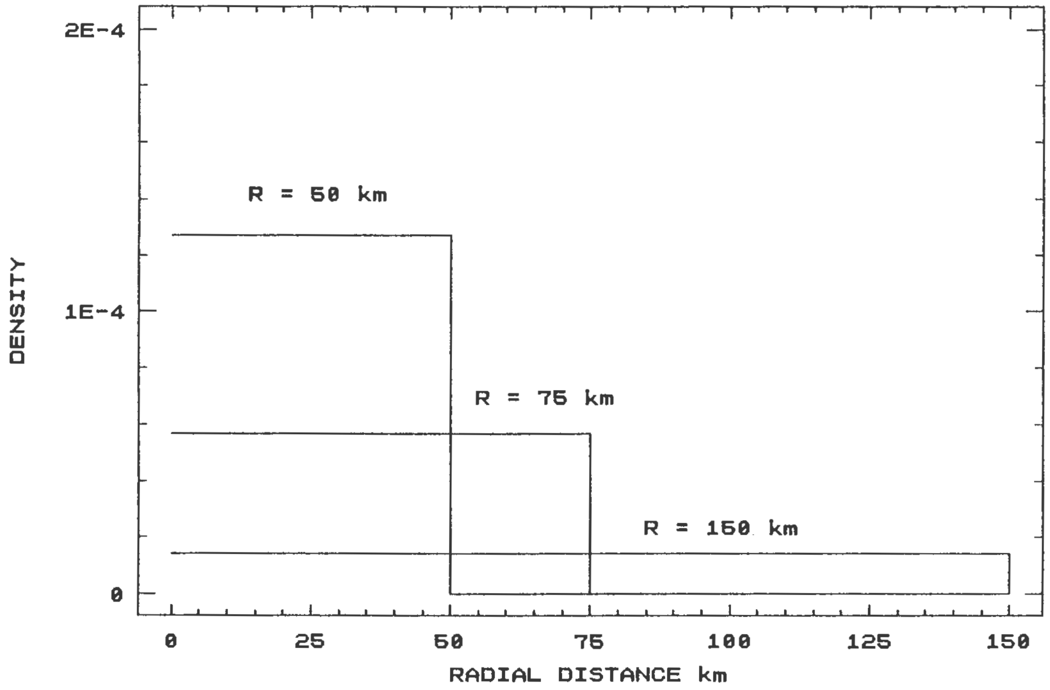


Figure 3.20 Model 1. Uniform disc density model. Density plotted against radial distance for three models: R = 50, 100 and 150 km.

For model 2) $ß = 2$ and $\tau = ½$ while for model 3) $ß = 2$ and $\tau = 1$. It can be shown that this generalized distribution also includes the Cauchy bi-variate distribution (Mardia 1970: 86):

$f(r) = (c/\{2*\pi\})/(r^2+c^2)^{3/2}$

5) Exponential decay:

$f(r) = \alpha*EXP(-ß*r)$. Where α and ß are suitable constants >0.

This model is intuitively appealing because f(0) is finite and $f(r)\to0+$ as $r\to\infty$. Given suitable values for α & ß the integral over the whole plane is unity.

6) Bivariate normal. From studies of animals foraging and of their space-time distribution in their home ranges it has been suggested that an appropriate model for the density is the bivariate normal (W. Zucchini and R. von Hensenburg pers. comm.). The full form of the bi-variate normal distribution may be found in Mardia (1970: 85), but assuming radial symmetry this reduces to:

$f(r) = (2\pi\sigma^2)^{-1}*EXP(-½*\{r/\sigma\}^2)$ Where σ^2 is the variance.

The assumption of radial symmetry implies that the mean, $\mu = 0$.

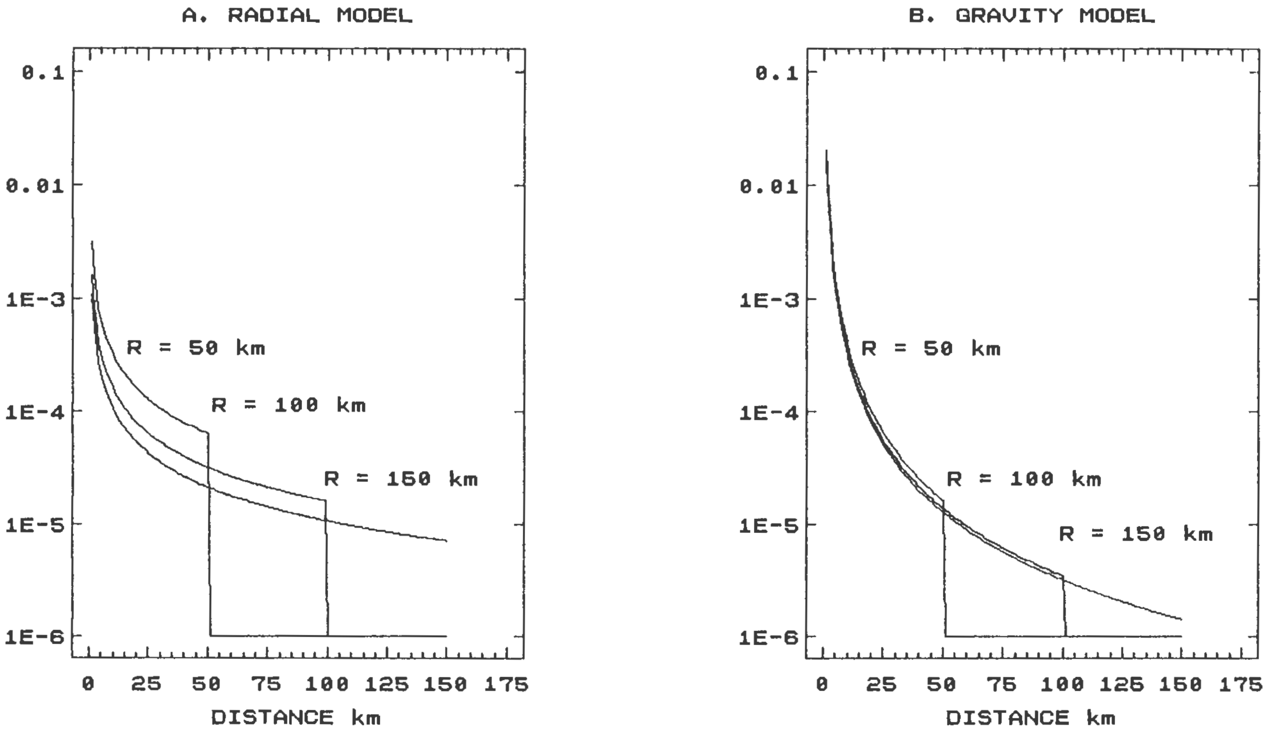


Figure 3.21 A. Model 2. Radial search model. B. Model 3. Gravitational attraction model. Density plotted against radial distance for three models: R = 50, 100 and 150 km.

Of the above, models 1), 4), 5) & 6) will under certain conditions, meet the requirements for finiteness and non-negativity. To ensure that their integrals over the whole plane sum to unity they must satisfy:

$$\int_0^{\infty}\int_0^{2\pi} f(r)\cdot r\cdot d\theta\cdot dr = 1$$

But f(r) is never a function of θ so this reduces to:

$$\int_0^{\infty} r\cdot f(r)dr\cdot \int_0^{2\pi} 1\cdot d\theta = 2\pi\cdot \int_0^{\infty} r\cdot f(r)\cdot dr = 1 \qquad \text{Equation 3.2.1.A}$$

This constraint, that the density function must integrate to unity over the whole plane, can be applied to each of the density functions. This constrains at least one of the parameters and makes the distributions slightly simpler to work with.

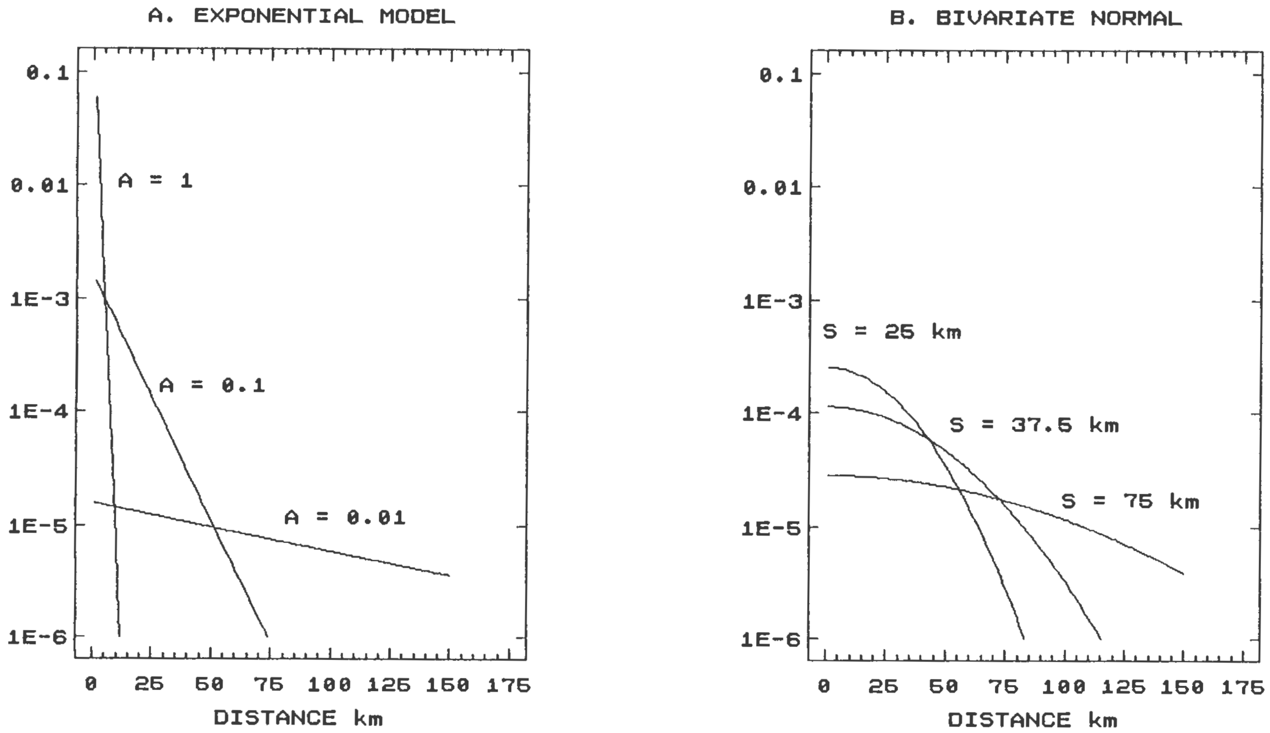


Figure 3.22 A. Model 4. Exponential decay model. Density plotted against radial distance for three models: A (= ß in equation) = 1, 0.1 and 0.01. B. Model 5. Bivariate normal model. Density plotted against radial distance for three models: S (= σ, variance in equation) = 25, 37.5 and 75 km.

1) For model 1 above f(r) = α over the range (0,R) and Equation 3.2.1.A becomes:

$$2\pi\cdot\int_0^R r\cdot f(r)dr = 2\pi\cdot\int_0^R r\cdot\alpha\cdot dr = \alpha\pi R^2 = 1$$

Hence $\alpha = 1/(\pi R^2)$. This is the expected result, i.e. it is the density resulting from averaging a bird over the whole area of the foraging disc, i.e πR^2. Thus, given a foraging radius, R the dispersion is completely specified. As examples, the density function is graphed for three values of R = 50, 75 and 150 km (Figure 3.20).

2) Substituting the generalized model 4 into Equation 3.2.1.A gives:

$$2\pi\cdot\int_0^\infty r\cdot f(r)dr = 2\pi\cdot\int_0^\infty r\cdot\alpha\cdot(r^{\beta}+\delta)^{-\tau}\cdot dr$$

There is no general formula (that I can find) for the kernel $r/(r^{\beta} + \delta)^{\tau}$. Thus the following special cases will be considered. Put $\beta = 2$ and $\tau = 1$. This reduces the above equation to:

$$2\pi \cdot \alpha \cdot \int_{0}^{\infty} r/(r^2+\delta) \cdot dr$$

The general form of this integral is $\frac{1}{2}\mathrm{Ln}(r^2 + \delta)$ (Petit Bois 1961: 4). Unfortunately this tends to infinity as the upper limit tends to infinity. Putting an upper limit to the foraging radius, $r = R$ gives:

$\pi^* \alpha^* \mathrm{Ln}(\{R^2 + \delta\}/\delta) = 1$

Hence:

$\alpha = [\pi^* \mathrm{Ln}(\{R^2 + \delta\}/\delta)]^{-1}$

Thus having chosen a suitable foraging radius, R a family of densities will be generated from a range of choices of δ.

Now consider the special case of $\beta = 2$ and $\tau = \frac{1}{2}$ and substitute into Equation 3.2.1.A:

$$2\pi \cdot \alpha \cdot \int_{0}^{\infty} r \cdot (r^2+\delta)^{-\frac{1}{2}} \cdot dr$$

The general form of this integral is $2\pi \bullet \alpha \bullet (r^2 + \delta)^{\frac{1}{2}}$ (Petit Bois 1961: 51). Again, this tends to infinity as the upper limit tends to infinity. Putting an upper limit to the foraging radius, $r = R$ gives:

$2\pi \bullet \alpha \bullet [(R^2 + \delta)^{\frac{1}{2}} - \delta^{\frac{1}{2}}] = 1$

Hence:

$\alpha = (2\pi)^{-1} \bullet [(R^2 + \delta)^{\frac{1}{2}} - \delta^{\frac{1}{2}}]^{-1}$

Thus having chosen a suitable foraging radius, R a family of densities will be generated from a range of choices of δ. These two density functions have been computed for three values of R = 50, 75 and 150 km (Figure 3.21).

3) For the exponential model $f(r) = \alpha \bullet e^{-\beta \bullet r}$ and substituting in Equation 3.2.1.A and using the product rule (Thomas 1960: 365) yields:

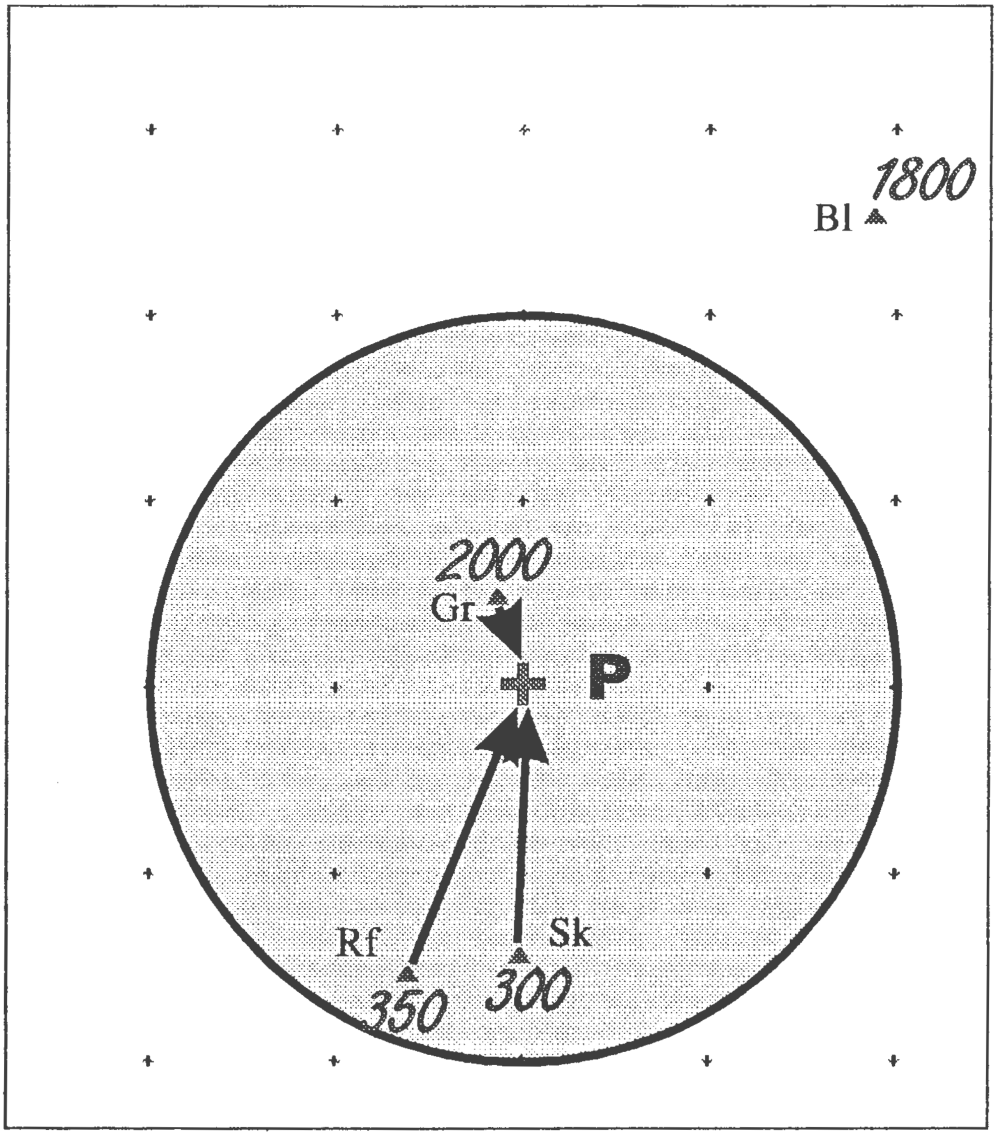


Figure 3.23 Uniform disc model of radius 150 km. There are three sites within 150 km radius of the large cross at the centre, i.e. point P. Sites shown: Roberts' Farm (Rf), Skeerpoort (Sk), Groothoek (Gr = Kransberg) and Blouberg (Bl).

$$2\pi\cdot\alpha\cdot\int_{0}^{\infty} r\cdot e^{-\beta\cdot r}\cdot dr = 2\pi\cdot\alpha/\beta^2 = 1$$

Thus $\alpha = \beta^2/(2\pi)$. Note the exponential distribution is a family of distributions, dependent on β. Choosing $\beta = 1$, 0.1 and 0.01 three density distributions are illustrated (Figure 3.22 A).

4) The bivariate normal distribution will take on the following form if the home-site is at the origin, i.e. this is the same as assuming that the mean, $\mu = 0$:

$$(\sigma^2)^{-1}\cdot\int_{0}^{\infty} r\cdot\exp(-\tfrac{1}{2}*(r/\sigma)^2)\cdot dr = (\sigma^2)^{-1}\cdot\sigma^2 = 1$$

From this it may be seen that the normal distribution is normalized! It too, is a family of distributions in that each value of the variance will give a different distribution. The variance, σ has the same units as the radial distance and acts, in a sense, as a scale factor. Choosing $\sigma = 25$, 37.5 and 75 km yields three density functions (Figure 3.22 B).

In the models described above there are no parameter-free distributions and it is necessary to have, at least, some idea of the maximum home-range, or foraging radius, R. How is R to be estimated? The largest value of R suggested to date for griffon vultures (R=150 km) comes from the study conducted by Pennycuick (1972) in East Africa of vultures foraging over the open plains. Other examples are 100 km from Mundy (1982), 200 km in Borello (1987) and the shorter distances of 25 km (Robertson & Boshoff 1986) and 50 km (Brown & Piper 1988).

Once the radial density distribution of Cape Vultures, f(r) from their central site (i.e. roost or colony) has been fixed it is possible to compute the theoretical density of Cape Vultures over all of southern Africa. Consider an arbitrary fixed point P (Figure 3.23) at spatial location (x,y). If the i^{th} Cape Vulture site has B_i birds resident and if the distance to the arbitrary point, P is r_i km then the density of Cape Vultures at P, from the i^{th} site will be $f(r_i)*B_i$. Thus the total density of Cape Vultures at point P will be the sum over all sites:

$$\Sigma_i\{f(r_i)*B_i\}$$

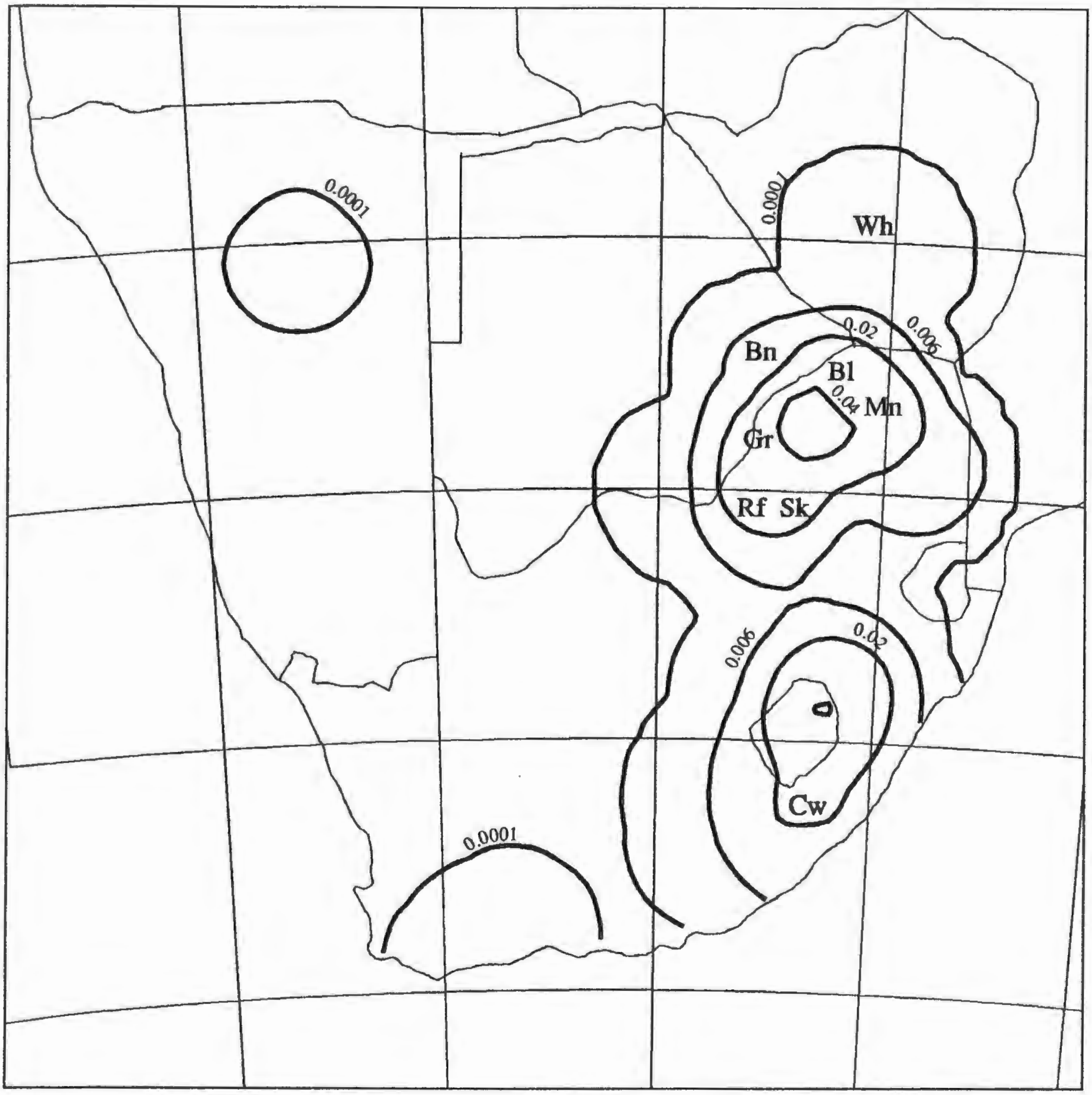
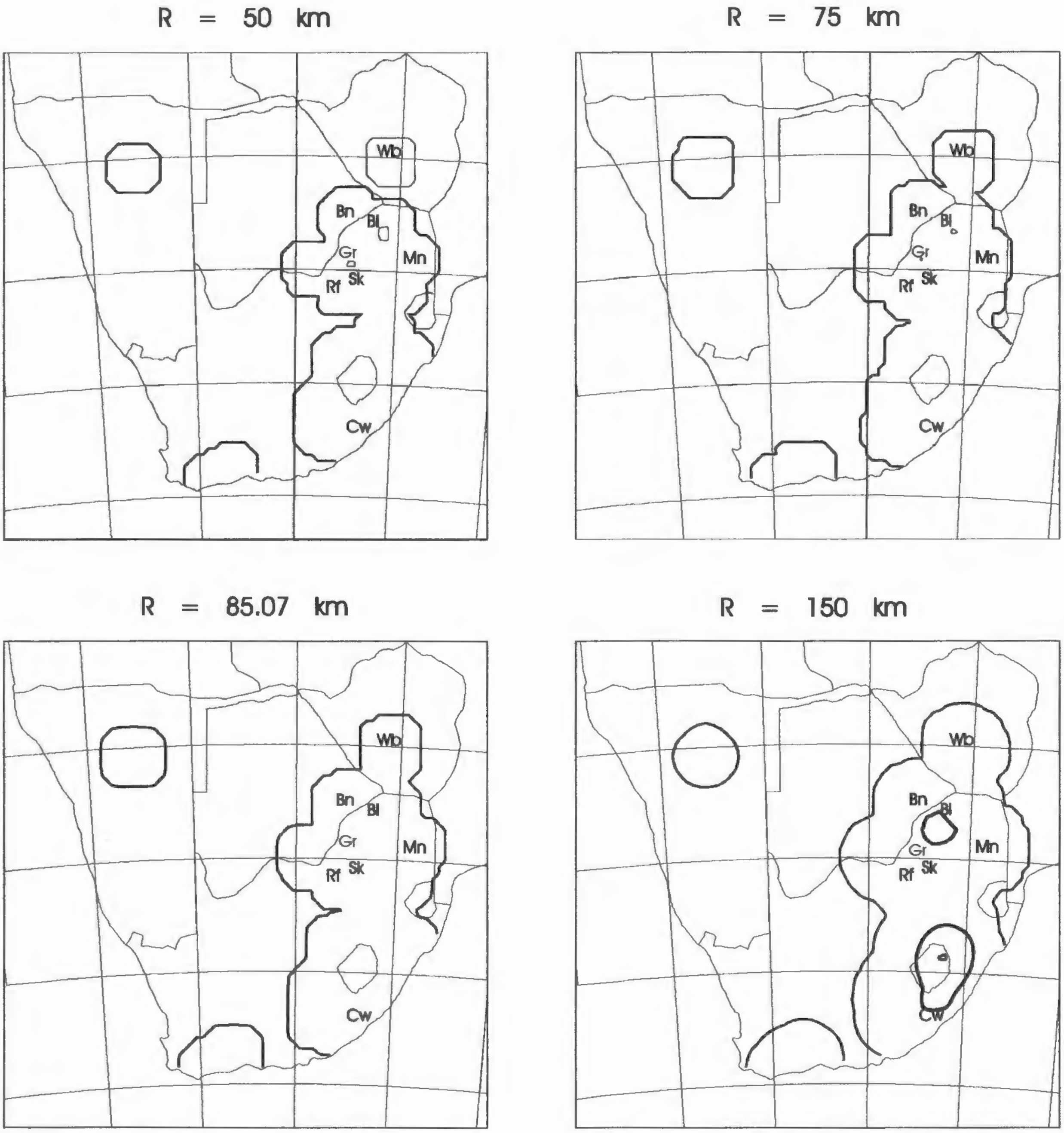


Figure 3.24 Density of Cape Vultures estimated from the uniform disc model of radius 150 km. Densities are in birds/km^2. To convert to biomass, as kg/km^2, multiply by 8.5. Sites marked are: Roberts' Farm (Rf), Skeerpoort (Sk), Groothoek (Gr = Kransberg), Blouberg (Bl), Manoutsa (Mn), Bonwalenong (Bn), Wabai Hill (Wh) and Colleywobbles (Cw).

This process of computing the density of vultures at any point may be extended to map the density of Cape Vultures over the whole sub-continent. The final map can be presented in a number of forms such as a contour map or a three dimensional (3-D) projection. The construction of such a density map is a four-step process.

1) Chose a suitable map surface. The Albers' Equal Area (AEA) map projection (see details in Appendix 1) at a map scale of 1 in 15 000 000 (i.e. 1 mm on the map equals 15 km on the ground) is to be used as the base map. This is one of the standard map projections used for small-scale mapping in southern Africa (D.A. Scogings pers. comm.). The scale used is such that the map of southern Africa (about 160 by 160 mm) fits neatly on a single A4 sheet while still leaving room for annotations. Details of computing coordinates and the mathematical transformations used to convert between geographical and map co-ordinates are fully described in Appendix 1.
2) Set up a grid. A grid of 2 by 2 mm is used. This results in a matrix of 81 rows by 81 columns (= 6561 points) which represents a grid of about 30 by 30 km on the ground and this is about ¼° of latitude by ¼° of longitude - the approximate area covered by a 1 in 50 000 map sheet such as those used for mapping bird distributions (see section 3.2.5 below).
3) Using the summation $\Sigma_i\{f(r_i)*B_i\}$ at each and every point on the grid it is possible to build up a regular matrix of densities. Using model 1, the uniform disc, with $R = 150$ km a matrix of population density has been created (Exhibit 3.2.1.1).
4) Using the matrix of densities it is possible to interpolate contours or construct 3-D views. The existence of a regular grid makes these computations much faster and more efficient. Using the grid described above a contour map has been constructed (Figure 2.24). The smallest sites have about 10 birds and spread over a disc of 150 km this gives densities of about 0.00014 birds/km^2. The biggest site (Groothoek) has 2000 birds and spread over a disc of radius 150 km this gives a density of about 0.028 birds/km^2. The maximum density on the map is just over 0.04 birds/km^2 and this is in the region between Groothoek, Blouberg and Manoutsa where their birds overlap.

By way of comparison four contour maps are produced using the uniform disc model with radii of 50, 75, 86 and 150 km (Figure 3.25). It will be shown below (section 3.2.11) that at a radius of 86 km the agreement between the SABAP sightings data and the uniform disc model is a maximum. It is seen for the case $R = 50$ km that the region around Wabai Hill forms an isolated island but this is not so for higher R. As R increases so the two concentrations centred in the Transvaal and Lesotho merge.


R = 50 km

R = 75 km

R = 85.07 km

R = 150 km

CVDIS

Figure 3.25 Comparison of density maps Cape Vultures estimated from the uniform disc model using radii of R = 50, 75, 86 and 150 km. The outer contour is at 0.0001 birds/km^2 and the inner (in the bottom left map) is at 0.04 birds/km^2. To convert to biomass, as kg/km^2, multiply by 8.5. Sites marked are: Roberts' Farm (Rf), Skeerpoort (Sk), Groothoek (Gr = Kransberg), Blouberg (Bl), Manoutsa (Mn), Bonwalenong (Bn), Wabai Hill (Wh) and Colleywobbles (Cw).

In order to model the Cape Vulture distribution using the these models estimates must be made of the parameters σ, α, ß, δ and τ; in other words, it is necessary to have some idea of the way Cape Vultures spread themselves out over the plane when they forage. To estimate these parameters there are two possible avenues which should be investigated: direct and indirect estimation.

Direct estimation. If it were possible to monitor a number of identifiable Cape Vultures over a reasonable period of time recording their geographical locations every short while then it might be possible to describe their average space-time distribution using one of the models described above. Unfortunately, only one radio-tracking study has been conducted to date (Boshoff, Robertson & Norton 1984) using a single Cape Vulture from the Potberg colony. No other density data are available for the Cape Vulture. Until such time as they are collected it will not be possible to use direct methods.

Indirect estimation. If it is assumed that bird-watchers see more Cape Vultures in areas where the density of birds is higher then it may be possible to estimate density in an indirect fashion. This will be investigated further in this chapter (see sections 3.2.5 and 3.2.11 below) using the SABAP sightings data.

In this section ways of taking the point count data and 'spreading the vultures out' over the plains have been considered. In order to decide which models are feasible and useful it is now necessary to turn to the sightings data from SABAP for they hold out hope for providing such a calibration tool.

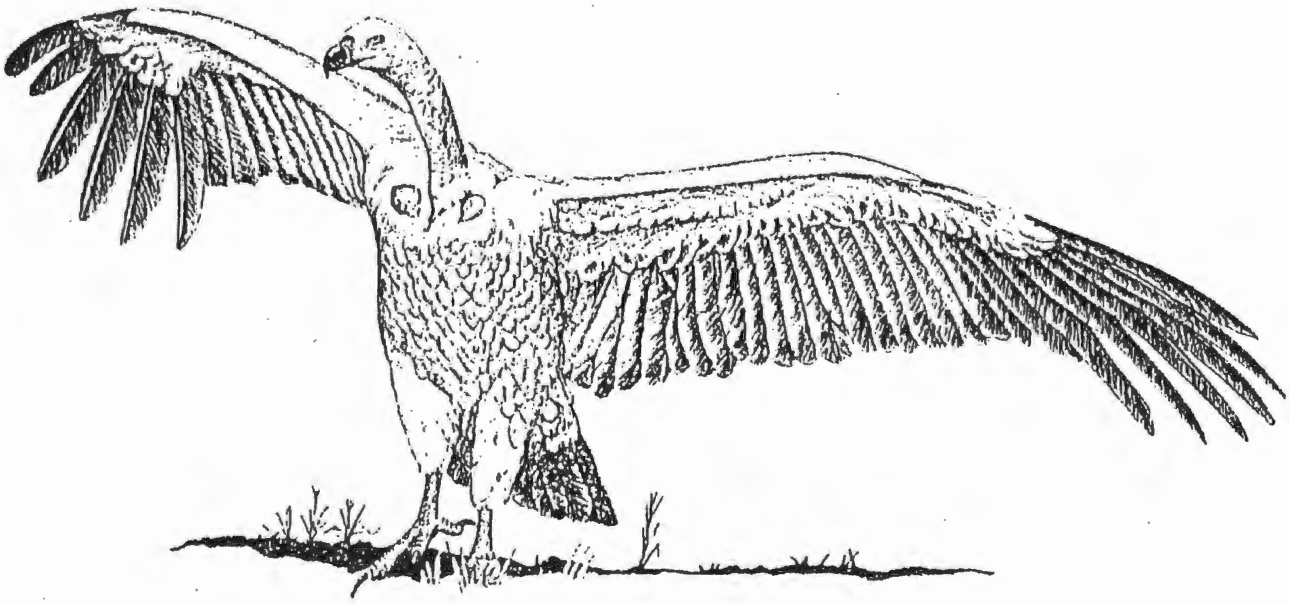


Exhibit 3.2.1.1

Stored as F:\MCAD\COL_DSC

Interpolates Cape Vulture density using a flat disc radius R0 km

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Constants used :		
	$Xmin \equiv -90$	Origin of the map, X
	$Ymin \equiv 0$	Origin of the map, Y
	$Scale := 15000000$	Scale of the map as 1 in Scale
	$Xmax \equiv 70$	Top right hand corner, X
	$Ymax \equiv 160$	Top right hand corner, Y
	$Dx \equiv 2$	X interval
	$Dy \equiv 2$	Y interval
	$Nx \equiv \mathrm{floor}\left(\frac{Xmax - Xmin}{Dx}\right) + 1$	No. X intervals
	$Ny \equiv \mathrm{floor}\left(\frac{Ymax - Ymin}{Dy}\right) + 1$	No. Y intervals
	$Nk := Nx \cdot Ny - 1$	Size of density matrix

$Nk = 6560$

$Nx = 81$ $Ny = 81$

Define the identities $k := 1$ $a := 1$ $b := 2$ $c := 3$ $d := 4$

$J(k) \equiv \mathrm{floor}\left(\frac{k}{Nx}\right)$ $I(k) \equiv k - Nx \cdot J(k)$

Read in the data

$R(a,b,c,d) \equiv \left[(a-c)^2 + (b-d)^2\right]^{\frac{1}{2}}$

$M := \mathrm{READPRN}(NBIRDS)$

Define radial distance $R0 := 85.0758$ km

$R1 := \frac{R0 \cdot 10^6}{Scale}$ $R1 = 5.672$ mm

Zero the density matrix

$k := 0, 1 .. Nk$

$D_k := 0$

Exhibit 3.2.1.1 (continued)

Compute the Xd and Yd values

$k := 0, 1 .. Nk$

$Xd_k := Xmin + Dx \cdot I(k)$

$Yd_k := Ymin + Dy \cdot J(k)$

$Rows := rows(M)$

$Cols := cols(M)$

Now unpack the colony data matrix

$i := 0, 1 .. Rows - 1$

$X_i := M_{i,0}$

$Y_i := M_{i,1}$

$N_i := M_{i,2}$

Now work through the colony matrix one colony at a time and one density at a time

$i := 0, 1 .. Rows - 1$

$k := 0, 1 .. Nk$

$$D_k := D_k + \frac{N_i \cdot if\left(R\left(X_i, Y_i, Xd_k, Yd_k\right) \le R1, 1, 0\right)}{\left(\pi \cdot R0^2\right)}$$

Write out the final data vectors

$WRITEPRN(CVDISCX) := Xd$

$WRITEPRN(CVDISCY) := Yd$

$WRITEPRN(CVDISD) := D$

Check that the total density adds up to about 12 000

$k := 0, 1 .. Nk$

$$\left(\sum_k D_k\right) \cdot 4 \cdot \frac{R0^2}{R1^2} = 12144.544$$

3.2.2 Distribution maps from sightings data

The desire to map the distributions of the southern African avifauna began with the compilation of 90 annotated species check-lists (as the South African Avifauna Series), initiated by J.M. Winterbottom and published by the Percy FitzPatrick Institute for African Ornithology in the 1960s and 1970s (see summary in Underhill, Oatley & Harrison 1991). This was followed by systematic 'atlasing' in Natal which increased rapidly in the 1970s culminating in the Natal Bird Atlas (Cyrus & Robson 1980). Since then atlasing has mushroomed in the subcontinent with separate atlases being published for the Transvaal (Tarboton, Kemp & Kemp 1987), Orange Free State (Earlé & Grobler 1987) and south-western Cape (Hockey, Underhill, Neatherway & Ryan 1989). At present draft atlases are in preparation for Lesotho (P. Osborne and B. Tigar pers. comm.) and Botswana (H. Penry, per H. Margeot pers. comm.). These disparate efforts are now combined into a single organisation: the Southern African Bird Atlas Project (SABAP: J. Harrison pers. comm.).

The need for a coordinated approach to mapping bird distributions grew out of a workshop on 'Bird Population Data-banks' held in Johannesburg in 1983 and addressed by R.J. O'Connor (then director of the British Trust for Ornithology). This was followed by a workshop, specifically on Bird Atlasing, held in Cape Town during 1984 (Hockey & Ferrar 1985). The SABAP project was formally launched in April 1986, and systematic subcontinent-wide data collection began in January 1987. The SABAP unit has been housed at the University of Cape Town since its inception and is presently (i.e. 1991) located at that University in the Department of Statistical Sciences. Computerization of all new data also began in January 1987 and since then historical data (i.e. pre-1987) for a number of regions have been computerized, or are in the process of being computerized (Harrison 1991).

As with many amateur-driven field projects spatial coverage is patchy and to remedy this a full-time, professional field-worker was appointed in April 1990. This has greatly increased coverage in those regions of particular importance to understanding the distribution of the Cape Vulture: Limpopo Valley, northern Cape, Transkei and Lesotho (D.G. Allan pers. comm.).

In the sections that follow the SABAP data will be examined and evaluated as to their suitability for predicting the spatial and temporal distributions of the Cape Vulture.

3.2.3 The SABAP data-set

The avifaunal field card data (also called check-list data) collected and housed in SABAP come from three zones:

1) That area falling into South Africa as of the 1960 Union of South Africa boundaries, i.e. including the so called 'independent states' and self-governing territories. This area is divided into nine regions, for atlasing purposes:

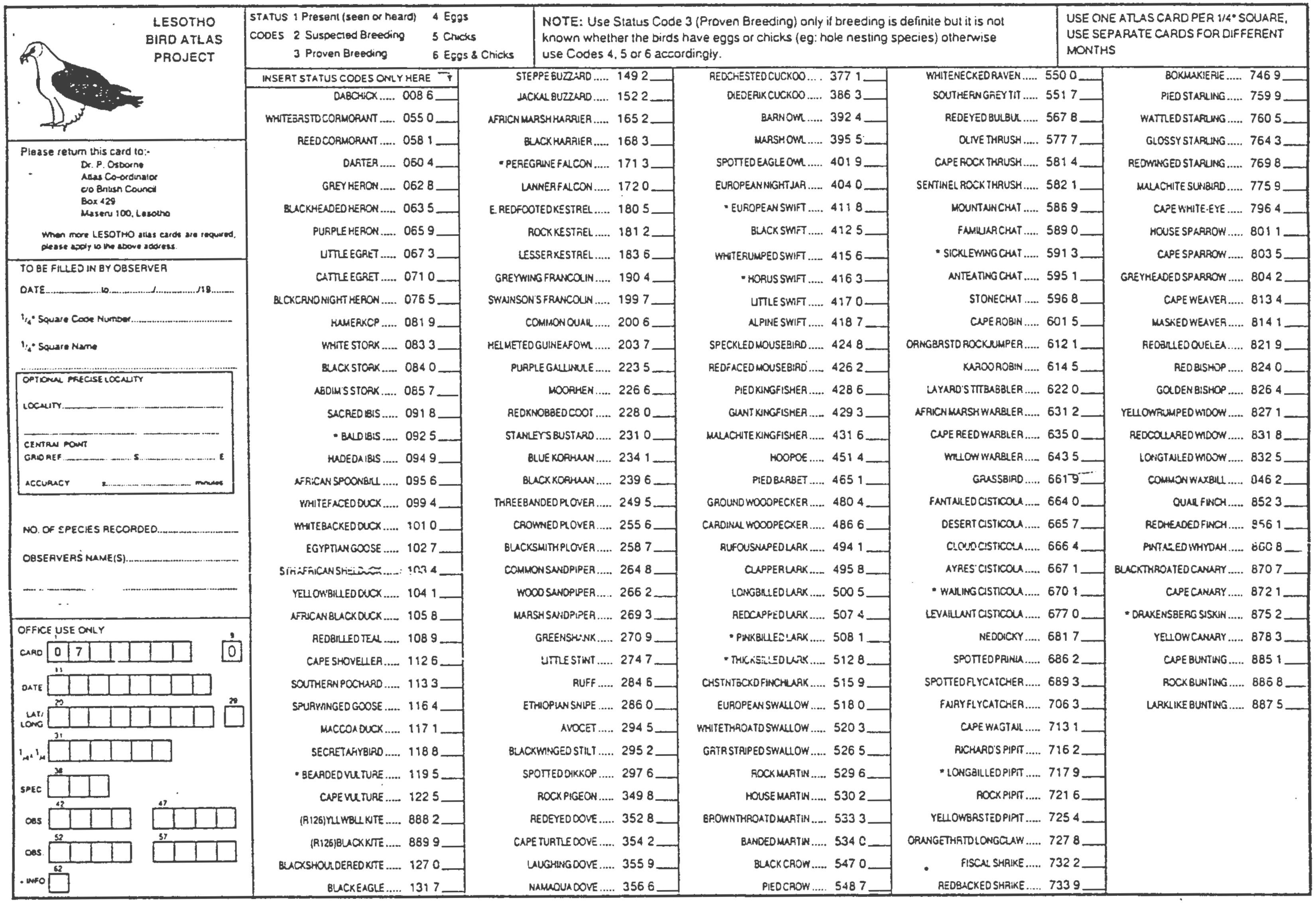
    western Cape, northern Cape, eastern Cape, Natal, Transvaal Lowveld, Orange Free State, southern Transvaal, northern Transvaal and north-east Transvaal.
2) Swaziland and Lesotho.
3) The adjoining countries: Namibia, Botswana and Zimbabwe.

Data from three adjoining countries (Namibia, Botswana and Zimbabwe) were not supplied to me by SABAP (for copyright reasons, P.J. Mundy pers. comm. and to protect the intellectual rights of Third World countries, C.J. Brown pers. comm.), but are to be requested from the SABAP once permission has been granted by their respective Regional Atlas Co-ordinators (RAC).

The avifaunal field card data are collected in the following manner:
Each observer making a list of birds seen on a field trip compiles a field card (see example in Figure 3.26) by filling in the following data-fields:

1) Locality: The ¼° by ¼° grid-cell reference (e.g. '2930DD') and its associated map name (e.g. 'Durban'. A field card is restricted to a maximum area of one ¼° by ¼° grid-cell; each grid-cell, in much of southern Africa is equivalent to a single 1 in 50 000 map sheet. It is possible to submit a field card for a smaller area.
2) Time: The start and end dates. The maximum time period for a field card is one calendar month.
3) Observer's name: The senior observer is responsible for the veracity of the data; additional observers' names may also be added.
4) Species: The 'new Roberts' number (i.e. Maclean 1985) is used.
5) Status code: The following codes are used:
    1 Present; seen or heard
    2 Suspected breeding
    3 Proven breeding
    4 Eggs
    5 Chicks
    6 Eggs and chicks
    7 Dependent fledglings

For checking purposes a species total is added.



LESOTHO
BIRD ATLAS
PROJECT

STATUS CODES 1 Present (seen or heard) 2 Suspected Breeding 3 Proven Breeding 4 Eggs 5 Chicks 6 Eggs & Chicks

NOTE: Use Status Code 3 (Proven Breeding) only if breeding is definite but it is not known whether the birds have eggs or chicks (eg: hole nesting species) otherwise use Codes 4, 5 or 6 accordingly.

USE ONE ATLAS CARD PER 1/4° SQUARE, USE SEPARATE CARDS FOR DIFFERENT MONTHS

Please return this card to:-
Dr. P. Osborne
Atlas Co-ordinator
c/o British Council
Box 429
Maseru 100, Lesotho

When more LESOTHO atlas cards are required, please apply to the above address.

TO BE FILLED IN BY OBSERVER

DATE..................to................/................/19.........

1/4° Square Code Number..................................

1/4° Square Name

OPTIONAL PRECISE LOCALITY

LOCALITY..................................

CENTRAL POINT
GRID REF.................S.................E

ACCURACY ±.................minutes

NO. OF SPECIES RECORDED..................

OBSERVERS NAME(S)..................

OFFICE USE ONLY

CARD	1	0 7		9	0
DATE	11				
LAT/LONG	20			29	
1/4, 1/4	31				
SPEC	38				
OBS	42			47	
OBS.	52			57	
+ INFO	62				

INSERT STATUS CODES ONLY HERE		STEPPE BUZZARD	149 2	REDCHESTED CUCKOO	377 1	WHITENECKED RAVEN	550 0	BOKMAKIERIE	746 9
DABCHICK	008 6	JACKAL BUZZARD	152 2	DIEDERIK CUCKOO	386 3	SOUTHERN GREY TIT	551 7	PIED STARLING	759 9
WHITEBRSTD CORMORANT	055 0	AFRICN MARSH HARRIER	165 2	BARN OWL	392 4	REDEYED BULBUL	567 8	WATTLED STARLING	760 5
REED CORMORANT	058 1	BLACK HARRIER	168 3	MARSH OWL	395 5	OLIVE THRUSH	577 7	GLOSSY STARLING	764 3
DARTER	060 4	* PEREGRINE FALCON	171 3	SPOTTED EAGLE OWL	401 9	CAPE ROCK THRUSH	581 4	REDWINGED STARLING	769 8
GREY HERON	062 8	LANNER FALCON	172 0	EUROPEAN NIGHTJAR	404 0	SENTINEL ROCK THRUSH	582 1	MALACHITE SUNBIRD	775 9
BLACKHEADED HERON	063 5	E. REDFOOTED KESTREL	180 5	* EUROPEAN SWIFT	411 8	MOUNTAIN CHAT	586 9	CAPE WHITE-EYE	796 4
PURPLE HERON	065 9	ROCK KESTREL	181 2	BLACK SWIFT	412 5	FAMILIAR CHAT	589 0	HOUSE SPARROW	801 1
LITTLE EGRET	067 3	LESSER KESTREL	183 6	WHITERUMPED SWIFT	415 6	* SICKLEWING CHAT	591 3	CAPE SPARROW	803 5
CATTLE EGRET	071 0	GREYWING FRANCOLIN	190 4	* HORUS SWIFT	416 3	ANTEATING CHAT	595 1	GREYHEADED SPARROW	804 2
BLCKCRND NIGHT HERON	076 5	SWAINSON'S FRANCOLIN	199 7	LITTLE SWIFT	417 0	STONECHAT	596 8	CAPE WEAVER	813 4
HAMERKOP	081 9	COMMON QUAIL	200 6	ALPINE SWIFT	418 7	CAPE ROBIN	601 5	MASKED WEAVER	814 1
WHITE STORK	083 3	HELMETED GUINEAFOWL	203 7	SPECKLED MOUSEBIRD	424 8	ORNGBRSTD ROCKJUMPER	612 1	REDBILLED QUELEA	821 9
BLACK STORK	084 0	PURPLE GALLINULE	223 5	REDFACED MOUSEBIRD	426 2	KAROO ROBIN	614 5	RED BISHOP	824 0
ABDIM'S STORK	085 7	MOORHEN	226 6	PIED KINGFISHER	428 6	LAYARD'S TITBABBLER	622 0	GOLDEN BISHOP	826 4
SACRED IBIS	091 8	REDKNOBBED COOT	228 0	GIANT KINGFISHER	429 3	AFRICN MARSH WARBLER	631 2	YELLOWRUMPED WIDOW	827 1
* BALD IBIS	092 5	STANLEY'S BUSTARD	231 0	MALACHITE KINGFISHER	431 6	CAPE REED WARBLER	635 0	REDCOLLARED WIDOW	831 8
HADEDA IBIS	094 9	BLUE KORHAAN	234 1	HOOPOE	451 4	WILLOW WARBLER	643 5	LONGTAILED WIDOW	832 5
AFRICAN SPOONBILL	095 6	BLACK KORHAAN	239 6	PIED BARBET	465 1	GRASSBIRD	661 9	COMMON WAXBILL	046 2
WHITEFACED DUCK	099 4	THREEBANDED PLOVER	249 5	GROUND WOODPECKER	480 4	FANTAILED CISTICOLA	664 0	QUAIL FINCH	852 3
WHITEBACKED DUCK	101 0	CROWNED PLOVER	255 6	CARDINAL WOODPECKER	486 6	DESERT CISTICOLA	665 7	REDHEADED FINCH	856 1
EGYPTIAN GOOSE	102 7	BLACKSMITH PLOVER	258 7	RUFOUSNAPED LARK	494 1	CLOUD CISTICOLA	666 4	PINTAILED WHYDAH	860 8
STH AFRICAN SHELDUCK	103 4	COMMON SANDPIPER	264 8	CLAPPER LARK	495 8	AYRES' CISTICOLA	667 1	BLACKTHROATED CANARY	870 7
YELLOWBILLED DUCK	104 1	WOOD SANDPIPER	266 2	LONGBILLED LARK	500 5	* WAILING CISTICOLA	670 1	CAPE CANARY	872 1
AFRICAN BLACK DUCK	105 8	MARSH SANDPIPER	269 3	REDCAPPED LARK	507 4	LEVAILLANT CISTICOLA	677 0	* DRAKENSBERG SISKIN	875 2
REDBILLED TEAL	108 9	GREENSHANK	270 9	* PINKBILLED LARK	508 1	NEDDICKY	681 7	YELLOW CANARY	878 3
CAPE SHOVELLER	112 6	LITTLE STINT	274 7	* THICKBILLED LARK	512 8	SPOTTED PRINIA	686 2	CAPE BUNTING	885 1
SOUTHERN POCHARD	113 3	RUFF	284 6	CHSTNTBCKD FINCHLARK	515 9	SPOTTED FLYCATCHER	689 3	ROCK BUNTING	886 8
SPURWINGED GOOSE	116 4	ETHIOPIAN SNIPE	286 0	EUROPEAN SWALLOW	518 0	FAIRY FLYCATCHER	706 3	LARKLIKE BUNTING	887 5
MACCOA DUCK	117 1	AVOCET	294 5	WHITETHROATD SWALLOW	520 3	CAPE WAGTAIL	713 1		
SECRETARYBIRD	118 8	BLACKWINGED STILT	295 2	GRTR STRIPED SWALLOW	526 5	RICHARD'S PIPIT	716 2		
* BEARDED VULTURE	119 5	SPOTTED DIKKOP	297 6	ROCK MARTIN	529 6	* LONGBILLED PIPIT	717 9		
CAPE VULTURE	122 5	ROCK PIGEON	349 8	HOUSE MARTIN	530 2	ROCK PIPIT	721 6		
(R126)YLLWBLL KITE	888 2	REDEYED DOVE	352 8	BROWNTHROATD MARTIN	533 3	YELLOWBRSTED PIPIT	725 4		
(R126)BLACK KITE	889 9	CAPE TURTLE DOVE	354 2	BANDED MARTIN	534 0	ORANGETHRTD LONGCLAW	727 8		
BLACKSHOULDERED KITE	127 0	LAUGHING DOVE	355 9	BLACK CROW	547 0	FISCAL SHRIKE	732 2		
BLACK EAGLE	131 7	NAMAQUA DOVE	356 6	PIED CROW	548 7	REDBACKED SHRIKE	733 9		

World Wildlife Fund

Figure 3.26 An example of a SABAP bird field card.

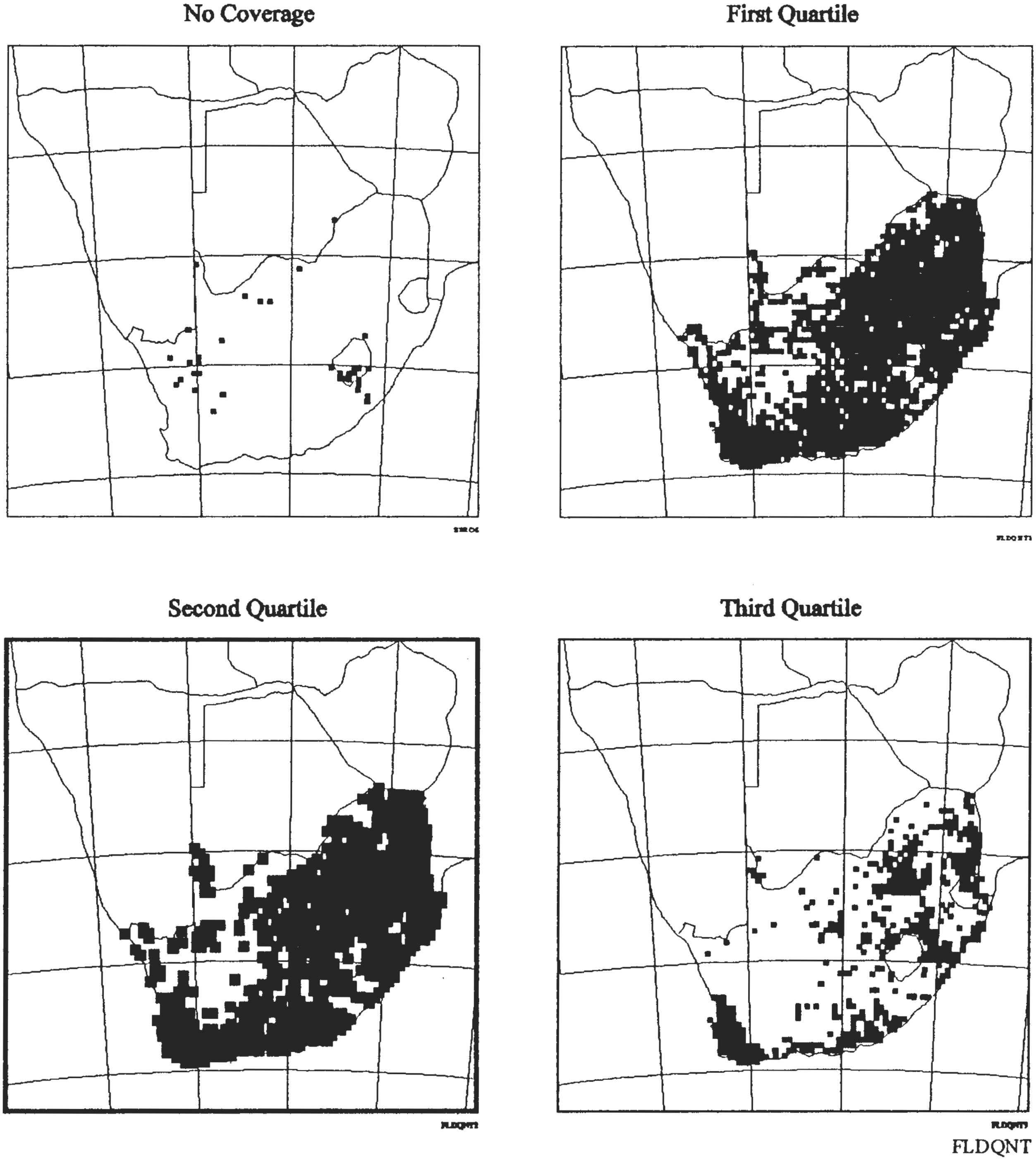


Figure 3.27 Characteristics of the SABAP data-set. A. Sites not visited. B. At least six field cards per grid-cell (= first quartile). C. At least 15 field cards per grid cell (= median). D. At least 46 field cards per grid-cell (= third quartile).

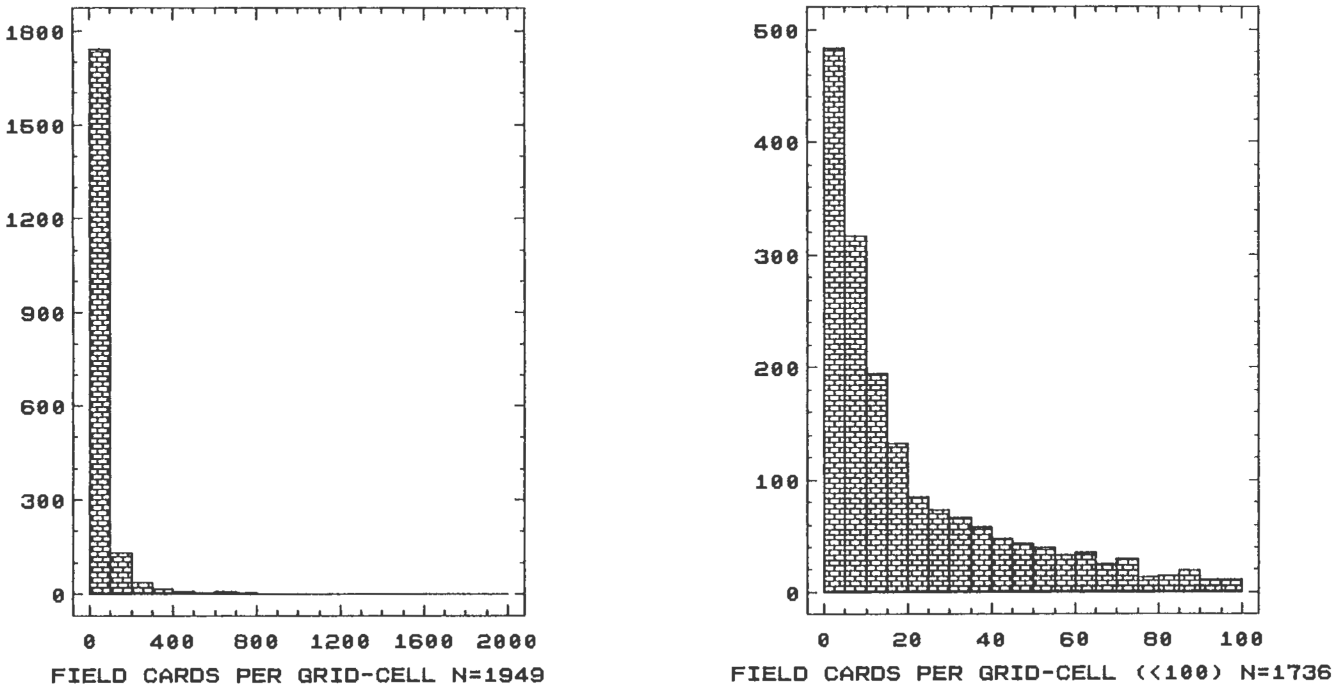


Figure 3.28 A. Number of field cards returned per grid-cell. B. As for A, but only for grid-cells with less than 100 field cards.

Given that this data-set is to hand an important question to ask is: What variations are to be found in the data?

These distributional data show four kinds of variation: those due to observer, species, weather and grid-cell.

1) Observer-induced variations result from the number of times a grid-cell is visited, the effort expended during a visit, the number of different months in which it is visited and the observer's ability to identify correctly the species to be mapped and to ascertain adequately their breeding status.
2) Species-specific variations are caused by real changes in the numbers of birds of a given species which are present in any grid-cell in any month of any year, their visibility in the various habitats of a grid-cell at the time of observation and the species' breeding activities then.
3) Environmental conditions, especially rain, wind and haze influence the extent to which birds come into the open, call and the ease with which an observer can view and identify them.
4) Birds are not all equally visible in all grid-cells. Some grid-cells have more open terrain, more roads, more vantage points, and are easier to search for birds than others.

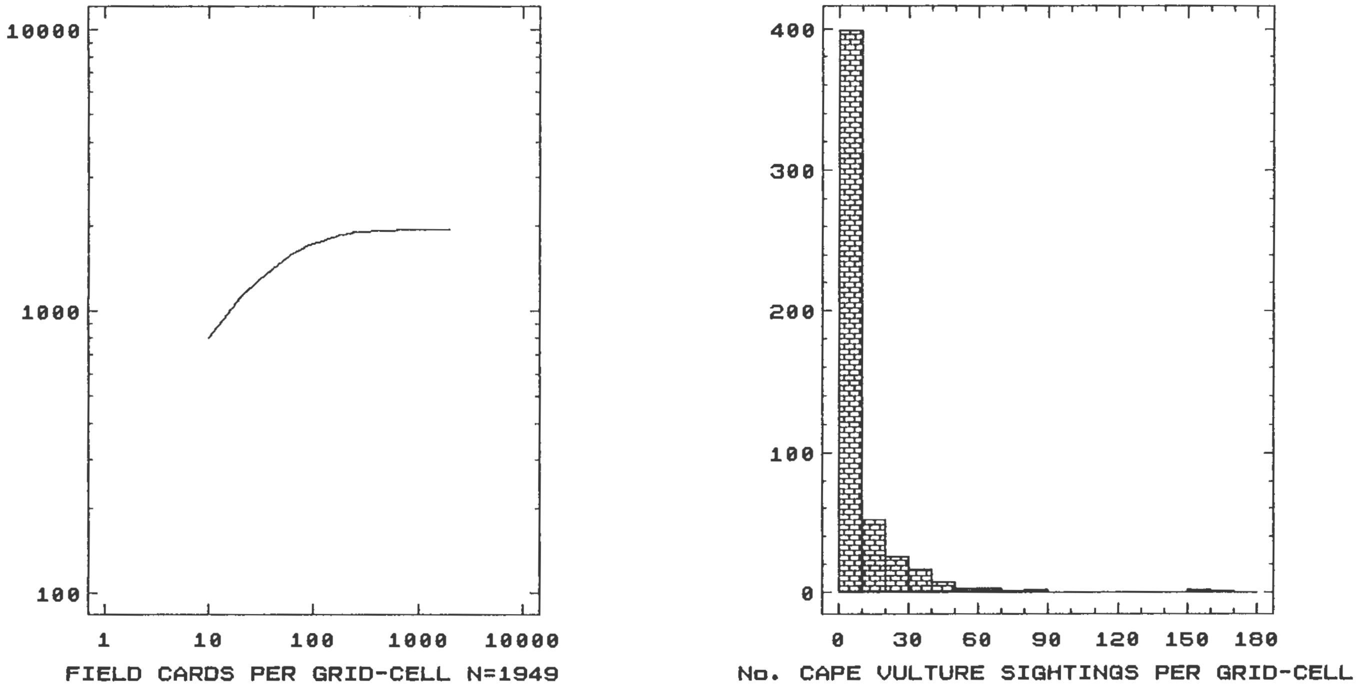


Figure 3.29 A. Cumulative number of field cards per grid-cell. B. Number of Cape Vulture sightings per grid-cell (N = 512).

Ways in which the adverse effects of observer-induced variations may be minimized, or even eliminated, will be discussed below. The analysis of seasonal, spatial and breeding variations are discussed in sections 3.2.4, .5 and .10 below. In the rest of this section a brief overview of the SABAP coverage is presented.

There are a total of 2 017 grid-cells in the SABAP data-set but 44 of these are from overlapping regions; thus there are 1973 unique grid-cells. No field cards were submitted for 35 grid-cells (Figure 3.27 A), i.e. the completeness of the coverage, as of 16 May 1991 was 98.2%. Most of the as yet to be visited grid-cells are in Transkei, Lesotho and the northern Cape.

The number of field cards submitted per grid-cell varied from one to 1956, though this was highly skewed (Figures 3.28 A & B and 3.29 A). Three-quarters of all grid-cells had 6 or more field cards, i.e. one every two months (Figure 3.27 B) with the major gaps being in the Transkei, Lesotho, northern Transvaal and Cape. Half of all grid-cells had 15 or more field cards (Figure 3.27 C), while only 25% had 46 or more (Figure 3.27 D); these being around the major metropolitan areas and in the more heavily 'touristed' nature reserves.

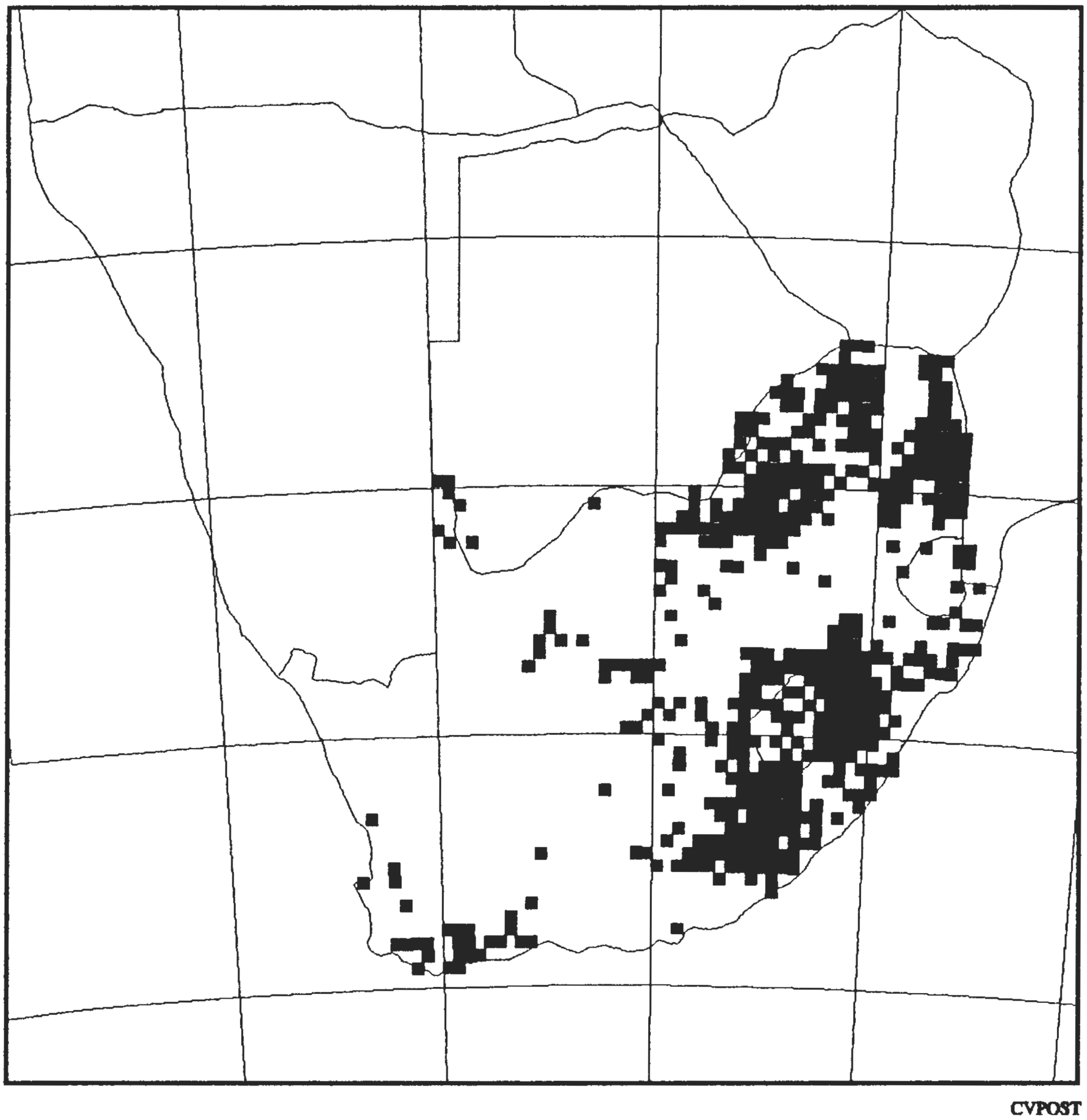


Figure 3.30 Presence and absence map of all Cape Vulture sight records in the SABAP data-set.

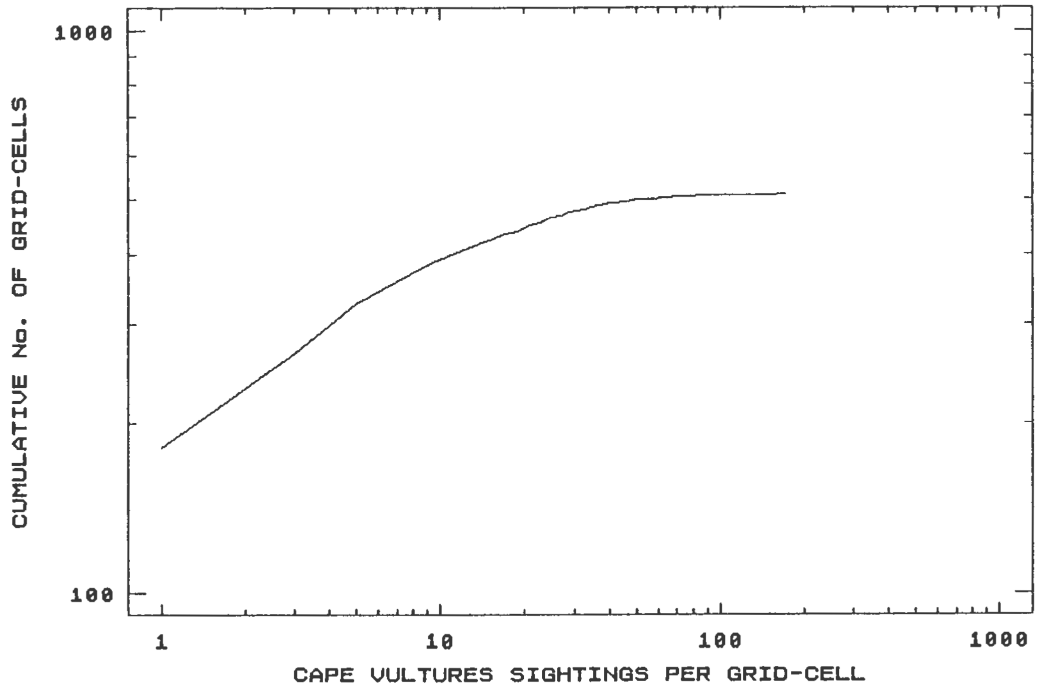


Figure 3.31 Cumulative number of Cape Vulture sightings per ¼° by ¼° grid-cell.

There were 512 non-overlapping grid-cells with at least one record of Cape Vulture (Figure 3.30). These were predominantly to the east of 25°E in Natal, Lesotho, Transkei, eastern Cape, north-eastern Transvaal and in the Lowveld. As with the numbers of field cards the numbers of Cape Vulture sightings were highly skewed. A quarter of all grid-cells with Cape Vultures recorded had only one sighting, half had two and less than a quarter had nine or more (Figure 3.31 A).

The 16 'holes' in the coverage (Figure 3.27 A) in Lesotho, Qwa Qwa, Natal and Transkei are a serious problem for mapping the distribution of the Cape Vulture because they occur in an area known to be in a secondary core of the population (section 3.2.1). The other 19 'holes' are much less important as they lie far outside the known range, but see below. The low coverage of most cells (Figure 3.27) represents a serious problem for the creation of an adequate index of reporting rate. A comparison of the presence and absence map (Figure 3.30) with the map of grid-cells with numbers of cards in the upper quartile (Figure 3.27 D) illustrates, dramatically, that the Cape Vulture exists predominantly outside the realm of the bird-watcher's popular haunts. This underlies a possible weakness in using the reporting rate as an index of abundance. The number of sightings of Cape Vultures per cell (Figure 3.31 A and B) follow a pattern similar to that of field cards submitted (Figure 3.28). Some of the ideas sketched here will be examined analytically in the sections that follow.

3.2.4 Seasonal variations

In compiling the Site Register it was noted that some observers thought that a number of roosts and colonies exhibited seasonal attendance by Cape Vultures (e.g. OFS - B.D. Colahan pers. comm.). Because the SABAP data are compiled on a monthly basis they are ideal for testing seasonality. The standard Chi-squared test for goodness-of-fit is used.

Chi-squared test.

The null hypothesis, H_0 is that the monthly reporting rate, p_i is constant throughout the year, i.e. H_0: $p_i = P$ (the average monthly rate) vs H_0 $p_i \# P$. The following terminology is defined for the ¼° by ¼° grid-cell under investigation:

Let r_i = No. of check-lists in month i reporting Cape Vulture: $1 \leq i \leq 12$
n_i = Total no. of check-lists in month i: $1 \leq i \leq 12$
$p_i = r_i/n_i$ = reporting rate for month i: $1 \leq i \leq 12$
$R = \Sigma r_i$ with the summation over all 12 months
$N = \Sigma n_i$
$P = R/N$ the average reporting rate
$e_i = n_i R/N$ = the expected number of check-lists showing Cape Vulture; being the average monthly reporting rate, weighted by month.

Chi-squared may be computed from:

$$\text{Chi-squared} = \Sigma(\{r_i - e_i\}^2)/e_i$$

This has 11 degrees of freedom and the critical value for the 5% tail is 19.6751.

It is known that chi-squared values are inflated if the expected values are less then 5. Thus, as a precaution, only those ¼° by ¼° grid-cells with more than 60 Cape Vulture sightings were selected, i.e. to give about five sightings per month. To my surprise there were only ten such sites (Table 3.17; Figure 3.32). Examining the whole data-set it may be seen that there are few ¼° by ¼° grid-cells (377 out of 1938 visited, i.e. 19.5%) with at least 60 check-lists.

Of the ten testable ¼° by ¼°grid-cells with at least 60 Cape Vulture sightings, four grouped together in the Transvaal around the Magaliesberg colonies, one in the O.F.S. near Bakerskop, two in Natal near 16 Cape Vulture sites and three in the Cape, one near Barkly East, one at Komga and one at Malgas where there are two Cape Vulture sites.

Table 3.17

List of ten ¼° by ¼° grid-cells with 60 or more Cape Vulture sightings

(First line = No. sightings; second line = No. check-lists)

No.	Map	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1	2527CD	21	16	11	9	11	14	16	13	19	14	12	10	166
		30	30	25	25	28	25	35	26	30	26	24	22	326
2	2527DB	5	3	2	5	7	5	6	9	9	7	8	5	71
		17	18	16	18	19	15	20	23	27	22	21	14	230
3	2527DC	6	5	8	7	5	5	11	5	9	12	5	6	84
		15	13	21	22	15	13	19	19	17	24	13	16	207
4	2527DD	15	17	13	13	12	13	9	12	12	12	15	10	153
		40	42	42	38	36	33	35	34	33	46	37	25	441
5	2829AC	3	4	5	6	4	4	8	8	5	5	3	5	60
		15	14	16	25	13	15	23	18	17	15	15	18	204
6	2929AB	5	2	6	7	7	5	8	3	7	4	4	8	66
		9	7	8	11	12	6	11	4	7	9	6	12	102
7	2929BC	3	7	6	10	7	5	5	5	12	4	3	2	69
		10	13	11	17	17	13	14	7	17	16	7	7	149
8	3027DC	4	6	6	3	4	5	5	6	7	8	6	8	68
		7	11	10	5	6	8	7	7	9	14	10	10	104
9	3227DB	6	5	4	3	5	1	10	10	9	11	11	7	82
		16	10	9	7	13	6	21	15	17	21	20	17	172
10	3420BC	13	15	15	11	10	8	14	11	17	16	16	14	160
		18	17	19	25	16	12	20	18	23	22	18	17	225

Each ¼° by ¼° grid-cell was tested using the chi-squared test for uniformity and all were found to be uniform (Table 3.18). Thus it may be concluded that the SABAP data do not exhibit any seasonality. However, if there is real seasonality it is not likely to be seen at these sites which are all near major colonies; noting, also, that these areas of high Cape Vulture counts are associated with intensive field work on behalf of the atlas teams. Thus the SABAP data are not sensitive enough to detect any such variations. However, it is possible that sacrificing spatial resolution could yield increased temporal resolution, i.e. by lumping together adjacent grid-cells there will be more temporal data per spatial unit[1].

---

[1] The SABAP team (J.A. Harrison, pers. comm.) lumped all the grid-cells in each atlasing region (approximating provincial boundaries) and found small seasonal variations in the Cape Vulture's reporting rate for the western Transvaal and Botswana (low reporting rate of 8% in January/February, high reporting rate of 10% in July/August) and eastern Cape (low reporting rate of 7½% in February to April, high reporting rate of 8 to 9% in August to October).

Table 3.18

Chi-squared test for uniformity of seasonal distribution at ten sites with more than 60 Cape Vulture sightings.

No.	Map	Chi-squared
1	2527CD	5.6533
2	2527DB	4.2762
3	2527DC	4.2453
4	2527DD	3.2900
5	2829AC	2.9241
6	2929AB	4.1632
7	2929BC	7.2591
8	3027DC	1.5581
9	3227DB	3.5611
10	3420BC	5.0446

(Chi-squared, 11 degrees of freedom, p>0.1 for all of the above)

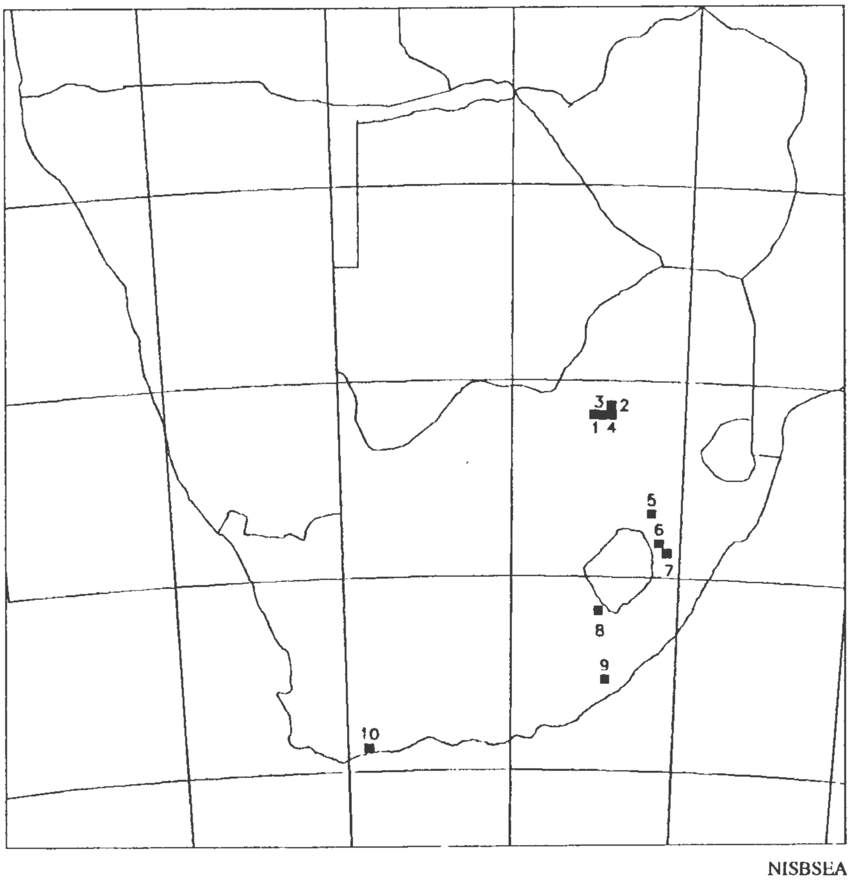


Figure 3.32 Spatial location of the 10 ¼° by ¼° grid-cells for which there were at least 60 check-lists reporting Cape Vultures by 16 May 1991.

3.2.5 Geographical variations

It was shown in the previous section that the SABAP data-set contained too few ¼° by ¼° grid-cells with sufficient temporal coverage of the Cape Vulture to elucidate any seasonal variations in Cape Vulture sightings. Thus all the monthly data for each ¼° by ¼° grid-cell have been coalesced to a single number of records of Cape Vultures, m_i out of a total of N_i field cards submitted for the i^{th} ¼° by ¼° grid-cell, i.e. this gives only one spatial distribution data-set for the Cape Vulture in southern Africa, not 12, distinct month-specific data-sets.

The presence and absence map of the Cape Vulture (Figure 3.30) does not give any idea of the (relative) density of this species and does not show the locations of this species' 'heartlands'. The highly speckled appearance of this map also makes it difficult to comprehend visually. The most important reasons for this are 1) The great variation in the number of times different ¼° by ¼° grid-cells were visited (Figure 3.28) and 2) The fluctuations in the proportions of field cards reporting Cape Vultures in each ¼° by ¼° grid-cell (Figure 3.33). To get a better measure of the spatial variation in the sightings of Cape Vultures four mapping methods are considered; these are all based on the concept of the reporting rate.

Method 1: Raw reporting rate.

If there are m_i sightings of Cape Vulture in the i^{th} ¼° by ¼° grid-cell out of a total of N_i field cards submitted for the i^{th} grid-cell then the raw reporting rate, $r_i = m_i/N_i$ is at best a measure, or an index, of relative abundance. Hopefully, if all else is constant, the reporting rate should indicate how the species' density, or some function of the species' density, varies across the subcontinent.

The most important assumption, when comparing reporting rates across ¼° by ¼° grid-cells which are far apart, is that the visibility of the species does not change across those habitat types in which it occurs. For many small avian species which use a variety of habitats this may not be true. The Cape Robin *Cossypha caffra*, for example, is easily seen on thinly treed mountains slopes and among the flotsam and jetsam of beaches, but it is well nigh impossible to find it in forests (T.B. Oatley pers. comm.; pers. obs.). But the Cape Vulture is a large, conspicuous bird of open plains and mountains and is highly visible over most of its range. Thus the assumption of constant visibility is not likely to be a major problem in interpreting the Cape Vulture reporting rate, though visibility and detectability may well be lower in its mountain fastnesses. More serious is the consistent under-reporting of Cape Vultures by bird-watchers because they tend to walk with their eyes on the ground, not in the heavens (P.J. Mundy pers. comm.).

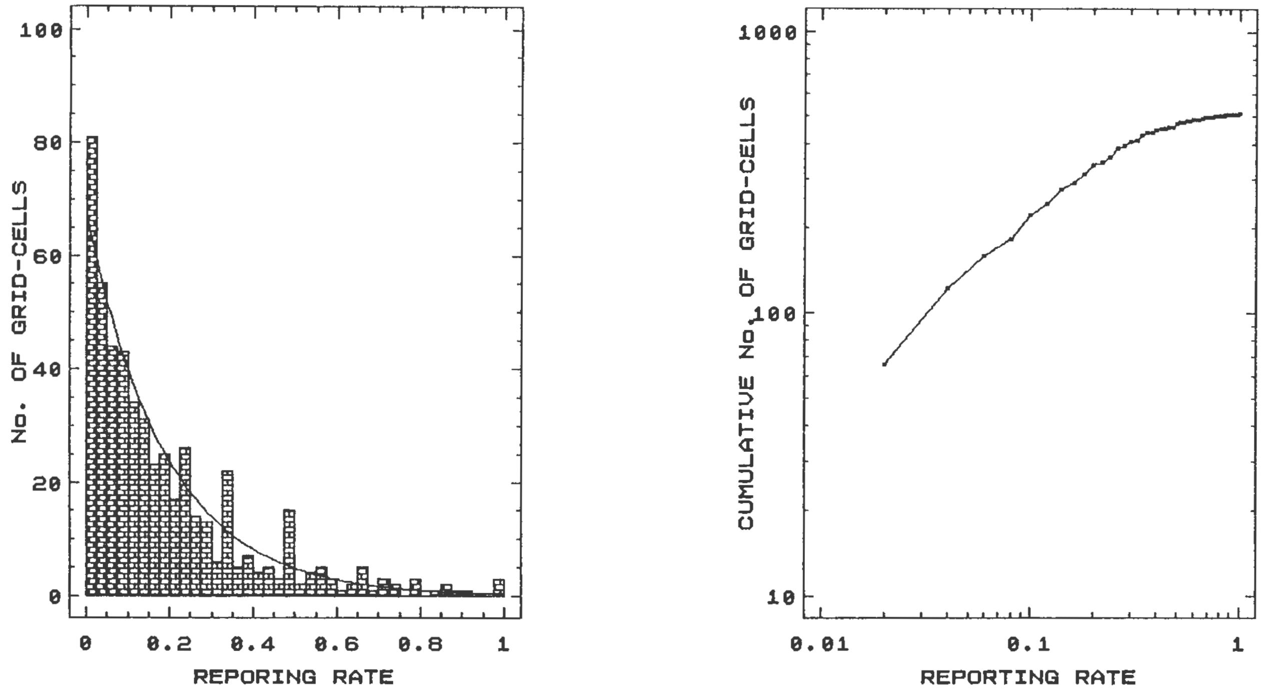


Figure 3.33 A. Distribution of the Cape Vulture reporting rate (as a fraction) overlaid with the best-fit exponential distribution. B. Cumulative distribution of the Cape Vulture reporting rate (as a fraction). N = 512 for both graphs.

A second assumption, which is made implicitly when computing reporting rates is that the persons compiling the field cards come from a random and homogeneous population of observers who have no great individual biases. The reporting rate must be, in some sense, a probability of seeing the species, within the whole guild of species seen. A counter example is a well-known field worker (who shall remain nameless) who, for many years, held the view that 'fish-eaters' were not true birds and so he had no cormorants on his own specially designed field cards (C.J. Vernon pers. comm.). Also excluded are special-purpose lists of the kind made by experts studying a single family of birds (e.g. the Stork Census; the Crane Census; the Vulture Study Group's 'colony census form' which asks for 'other species'), bird-ringers (whose sampling strategy is not compatible with atlasing), and oologists who are concerned only with breeding records. This is not to say that most bird watchers are unbiased, of course they are, hence their consistent underreporting of certain species (e.g. Booted Eagle and flufftails). Rather, it is assumed that such biases as exist do not show any marked tendency to be clumped, in space or time, for any given species. Without this assumption (i.e. of largely unbiased observers across a whole taxon) it is not possible to use reporting rates when plotting distributions and this gives rise to many of the difficulties faced by plant conservationists (e.g. Hall 1989) who have to use the raw sightings data.

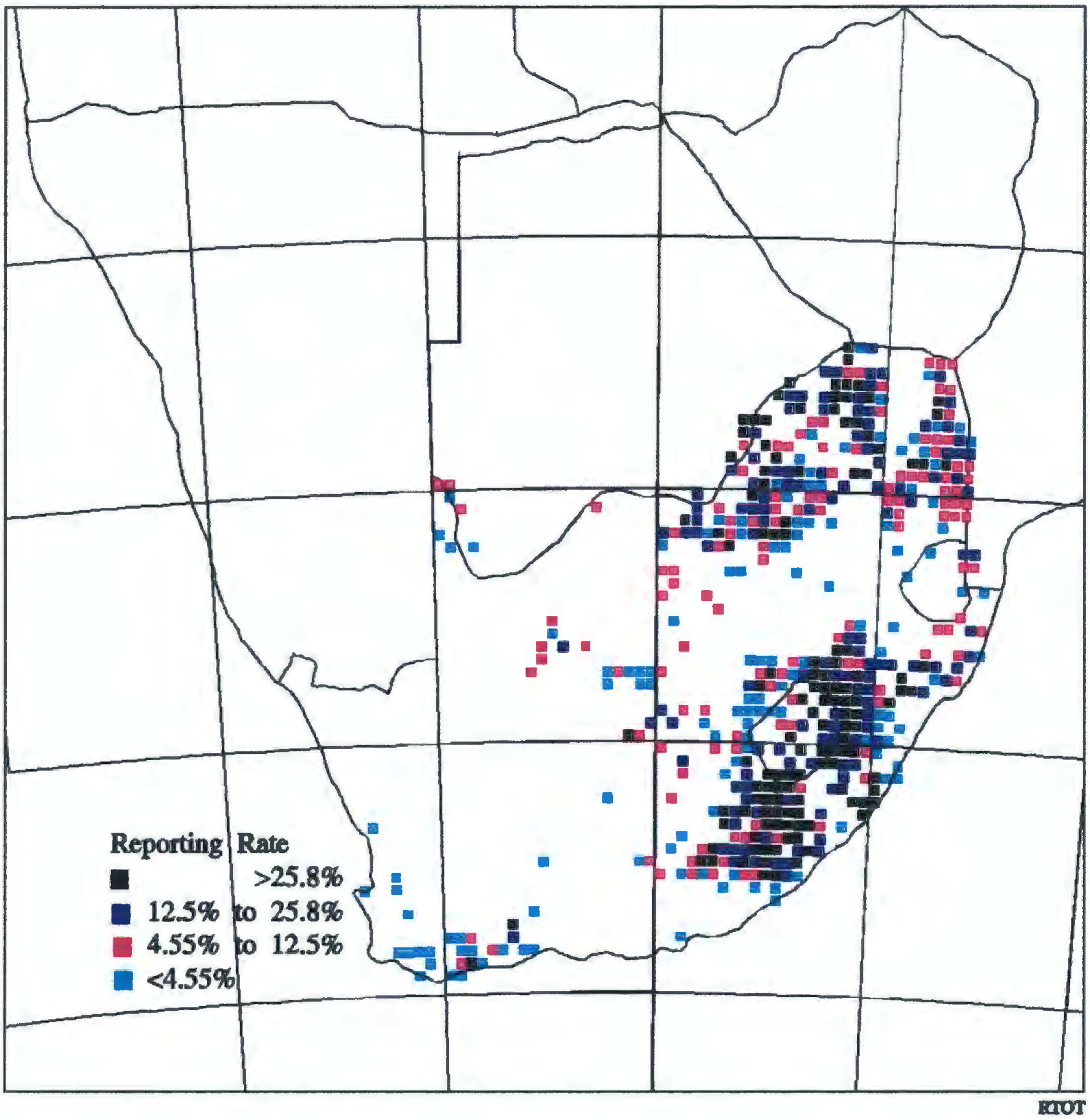


Figure 3.34 Cape Vulture reporting rate by ¼° by ¼° grid-cell portrayed as a grey-scale.

For the 512 ¼° by ¼° grid-cells in which the Cape Vulture was recorded the reporting rate varies from 0.00163399 to 1 with a median of 0.125 and a mean of 0.19, but the distribution is highly skewed (Figure 3.33). The lower quartile is 0.0455 while the upper quartile is only 0.25835 (Table 3.19). The distribution of reporting rates may be adequately described by an exponential distribution (Chi-squared = 4.3, 7 df, $p>0.8$; for fitted exponential curve see Figure 3.33 A).

Two technologies will be used to portray sightings and reporting rates: grey scale (or pseudocolour) raster maps and vector contour maps (see section 3.2.9 below for details). Suffice it to say here that the construction of contours implies some form of interpolation, and hence smoothing. Thus grey-scale maps must be used to portray the raw reporting rate. Using the raw reporting rate for each ¼° by ¼° grid-cell it is possible to construct a grey-scale map (Figure 3.34). In this map field cards are grey-scale coded so that those ¼° by ¼° grid-cells with no Cape Vultures reported appear pure white and those with a reporting rate of 100% appear pure black. The intermediate reporting rates are given an intermediate grey value.

Table 3.19

Percentiles for field cards, Cape Vulture sightings and raw reporting rate.

Percentiles	Field cards	Cape Vulture sightings	Raw reporting rate
0.5	1	1	0.00163399
1.	1	1	0.00318471
2.5	1	1	0.00480769
5.	2	1	0.00877193
10.	3	1	0.016129
25.	6	1	0.0454545
50.	15	2	0.125
75.	46	9	0.258343
90.	106	23	0.491228
95.	176	35	0.6
97.5	254	50	0.75
99.	508	71	0.861111
99.5	512	153	1.0

Method 2: Local smoothing of reporting rate.

The central problem with interpolating reporting rates comes from the nature of binomial sampling needed to estimate a rate, or more strictly, a proportion. To illustrate this problem consider that five samples (= number of field cards) of size 2, 5, 10, 50 and 100 are drawn from a grid-cell in which the probability of seeing a Cape Vulture is 50%. The following data are an example of the probable outcomes (simulated using a random number generator; confidence limits from Diem & Lentner 1970: 85 ff.):

Sample size *	Cape Vultures seen	Reporting rate	95% Confidence limits on reporting rate	
2	2	100%	15.8%	100.0%
5	3	60%	14.7%	94.7%
10	3	30%	6.7%	65.3%
50	26	52%	37.4%	66.3%
100	48	48%	37.9%	58.2%

* Sample size = No. of field cards

The larger the sample, i.e. the greater the number of field cards, the closer the reporting rate is likely to be to the true value and the tighter the confidence limits. In other words while 5/10, 50/100 and 500/1000 are all 50%; they are not the 'same 50%'. Thus it is necessary to seek ways of increasing the effective sample size so as to increase the precision of the reporting rate estimate.

If $r_1 = m_1/N_1$, $r_2 = m_2/N_2$, ... $r_n = m_n/N_n$ is a sample of n independent reporting rates drawn from the same population with a population reporting rate, R then it can be shown that the maximum likelihood estimate of the population reporting rate, R is $\Sigma m_i/\Sigma N_i$. The following example of five random samples, all of size 10, drawn from a grid-cell with a reporting rate of 10% illustrates this (simulated using a random number generator; confidence limits from Diem & Lentner 1970: 85 ff.):

Sample	A	B	C	D	E	Pooled
Field cards:	10	10	10	10	10	50
Cape Vultures:	2	2	1	2	1	8
Reporting rate:	20%	20%	10%	20%	10%	16.0%
95% Lower limit	2.5%	2.5%	0.3%	2.5%	0.3%	7.2%
95% Upper limit	55.6%	55.6%	44.5%	55.6%	44.5%	29.1%

The pooled estimate (i.e. 16%) has much tighter confidence limits (at about ±10%) than the individual estimates (more than ±20%). Thus local smoothing is an approach worthy of consideration and is implemented by choosing a small neighbourhood around a point and estimating the reporting rate for that point from the ratio $\Sigma m_i/\Sigma N_i$, where summation is over all points in the neighbourhood.

As a practical example consider a set of three by three ¼° by ¼° grid-cells just north of the Roberts' Farm Cape Vulture colony:

Legend
Map
$m_i/N_i=r_i$
95% Low &
95% high

2527AC 35/156=22.4 16%-30%	2527AD 32/173=18.4% 13%-26%	2527BC 6/68=8.8% 3%-18%
2527CA 29/330=8.7% 6%-12%	2527CB 20/114=17.5% 11%-26%	2527DA 1/18=5.5% 0.1%-27%
2527CC 8/44=18.1% 8%-33%	2527CD** 166/326=50.9% 44%-56%	2527DC 84/207=40.5% 33%-47%

** Location of the Roberts' Farm colony.

There is an important Cape Vulture colony in the ¼° by ¼° grid-cell 2527CD which is well known to the Witwatersrand Bird Club members who are responsible for atlasing this area; this colony has been the subject of Cape Vulture ringing expeditions for over 30 years, it is clearly visible from the main road which passes close by and yet Cape Vultures only appear on 50% of the field cards! Even more remarkable is how fast the reporting rate falls off with distance, especially as one goes north of the Magaliesberg. By combining the nine ¼° by ¼° grid-cells, the grouped estimate of the reporting rate is 381/1436=26.53% with 95% confidence limits of 24.25% to 28.81%; again tighter confidence limits than for any individual cell. Thus if a small, square mask is allowed to move across the spatial data-set and the ratio smoothed locally under its footprint, then a more uniform map should be produced.

Before blindly applying this technique the question to ask is: 'How big an area over which to smooth?' It is known from radio-tracking and glider-pilot observations that griffons from a breeding colony can easily travel up to 150 km in a single day and that is equal to about five ¼° by ¼° grid-cells (a more detailed discussion of the likely foraging radius is presented in section 3.2.1 above). Thus masks varying in size from (3 by 3) to (11 by 11) grid-cells could be considered. The manner in which a square mask is applied to the reporting rate data is illustrated below (Exhibit 3.2.5.1).

By smoothing the raw reporting rates using a uniform 3 by 3 mask and then contouring them yields a picture which is similar to that produced by using the raw reporting rates directly (Figures 3.34 and .35 A).

Method 3: Center-weighted smoothing of reporting rate.

Given that some form of smoothing is desirable to remove the stochastic variations resulting from small samples (i.e. too few field cards), it is necessary to consider what sorts of smoothing masks could be used. If Cape Vultures forage out from a roost or colony up to 150 km it is unlikely that their distribution over the plain will be uniform, but that is what is implied by a uniform mask. In my opinion, it is more likely that the distribution will have a cross section that tends to $1/d^{\alpha}$ where d = distance from roost and α is a constant, probably in the range 1 to 2. The distribution could also be bivariate normal. Following the line of argument motivating the use of a uniform mask above, a weighted reporting rate can be estimated from $(\Sigma w_i * m_i)/(\Sigma w_i * N_i)$; where w_i is a 'mask', or set of weights appropriate to the center-weighting function used, m_i is the number of Cape Vulture sightings in the i^{th} grid-cell and N_i is the number of field cards submitted. Masks typically used for spatial smoothing in digital image processing and remote sensing (also called convolution, Gonzalez & Wintz 1983) are:

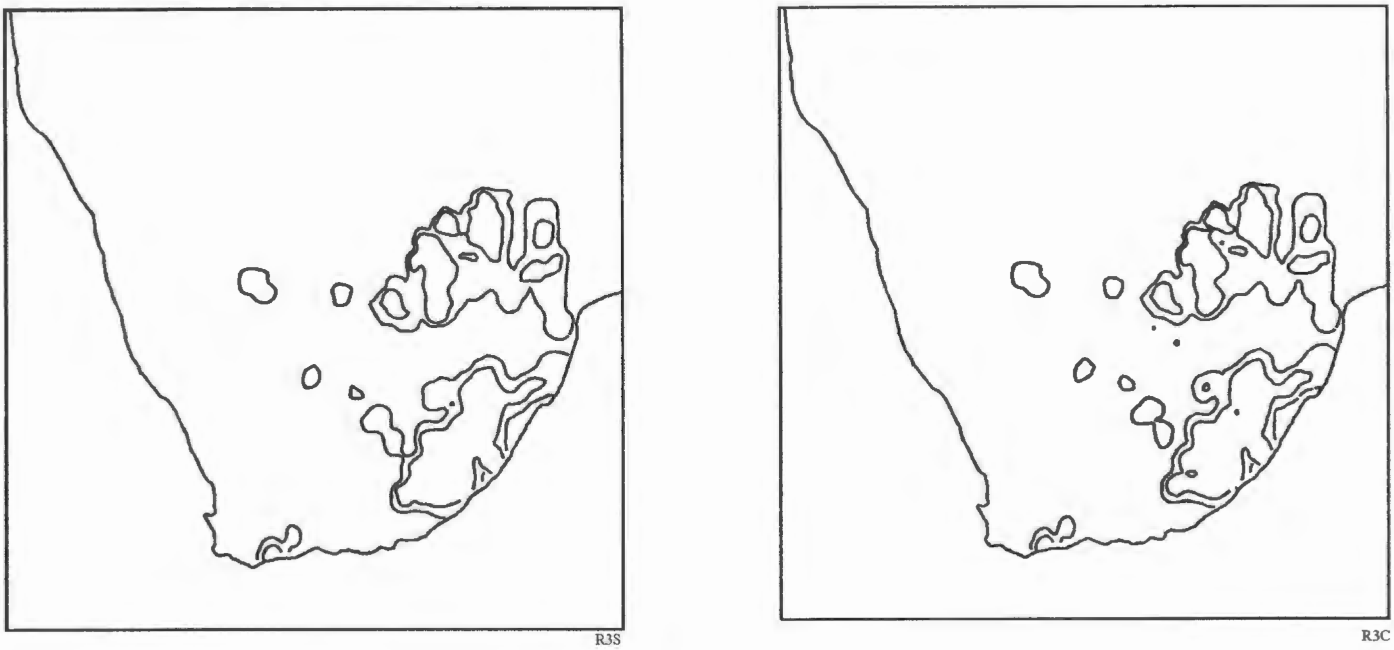
A)

$$w = \begin{bmatrix} 1 & 2 & 1 \\ 2 & 4 & 2 \\ 1 & 2 & 1 \end{bmatrix}$$

B)

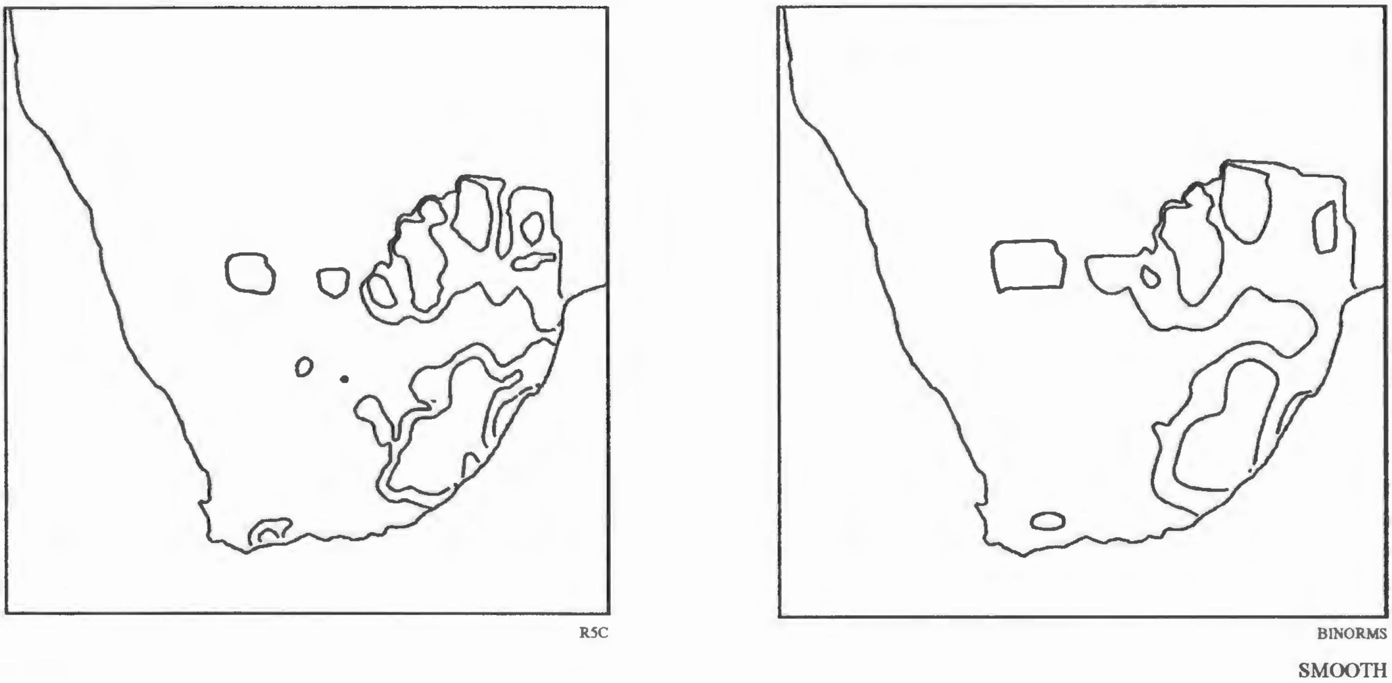
$$w = \begin{bmatrix} 1 & 2 & 4 & 2 & 1 \\ 2 & 4 & 8 & 4 & 2 \\ 4 & 8 & 16 & 8 & 4 \\ 2 & 4 & 8 & 4 & 2 \\ 1 & 2 & 4 & 2 & 1 \end{bmatrix}$$

Applying the centre-weighted 3 by 3 mask (i.e. A) yields a contour map that is not as smooth as that produced by the uniform mask (Figures 3.35 A and B). This is to be expected as the centre-weighted mask gives lower weight to the distant elements, i.e. it provides less smoothing. The centre-weighted 3 by 3 mask also produces five more 'islands' and 'peaks'. Applying the centre-weighted 5 by 5 mask (i.e. B) gives a map with much smoother contours and fewer island and peaks (Figure 3.35 C). It also plots the 3% contour slightly further out, i.e. the smoothing process 'spreads out' the sightings.



A) Uniform 3 by 3

B) Centre-weighted 3 by 3



C) Centre-weighted 5 by 5

D) Bivariate normal 9 by 9

Figure 3.35 Cape Vulture reporting rate shown as a contour map after smoothing the raw reporting rates using four different masks. A. Uniform mask of size (3 by 3). B. Centre-weighted mask of size (3 by 3). C. Centre-weighted mask of size (5 by 5). D. Bivariate normal mask of size (9 by 9). The two contours are at reporting rates of 3% and 12.5%

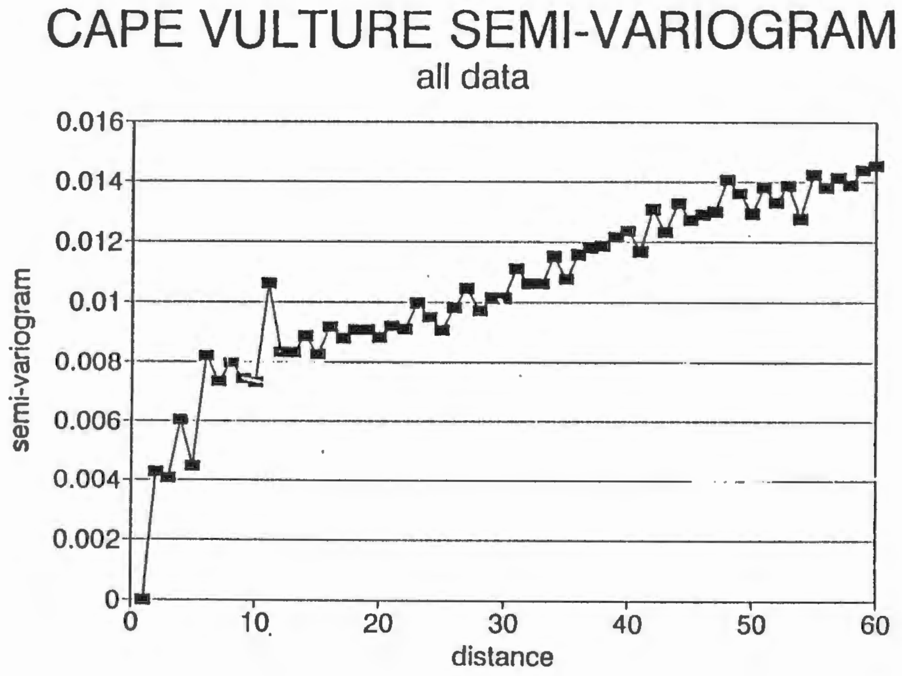


Figure 3.36 Semi-variogram using all the data and including null data. (Graphic drawn by L. McNeill.)

A bivariate normal mask may be constructed in the following fashion. Assume that the standard deviation, σ, of the distribution is the same in both directions and is, furthermore, measured in grid-cells. Let the mean in x and y be 0, i.e. in the centre of the grid-cell about which the smoothing takes place. If the mask is defined in terms of grid-cells then it may be indexed on i in the x-direction and j in the y-direction:

$$w_{i,j} = \int_{i+\frac{1}{2}}^{i+\frac{1}{2}} \int_{j+\frac{1}{2}}^{j+\frac{1}{2}} f(x,y)dxdy$$

where $f(x,y) = (2\pi\sigma^2)^{-1} * \mathrm{EXP}(-\frac{1}{2} * \{x^2+y^2\}/\sigma^2)$ Mardia (1970: 85)

It can be shown that if 95% of birds from a colony are to be found within a foraging radius of 150 km and their distribution is normal then σ will be approximately 61.3 km. If the length of ¼° of arc along a meridian is about 27.7 km then σ is about 2.2 units when measured in grid-cells. Using this value for σ a 9 by 9 mask has been constructed (Exhibit 3.2.5.2) and applied to the reporting rate data (Figure 3.35 D). It can be seen the smoothing is excessive and much of the fine structure is lost. In particular, the two major regions (i.e. those based on Transvaal and on Lesotho) are merged into one.

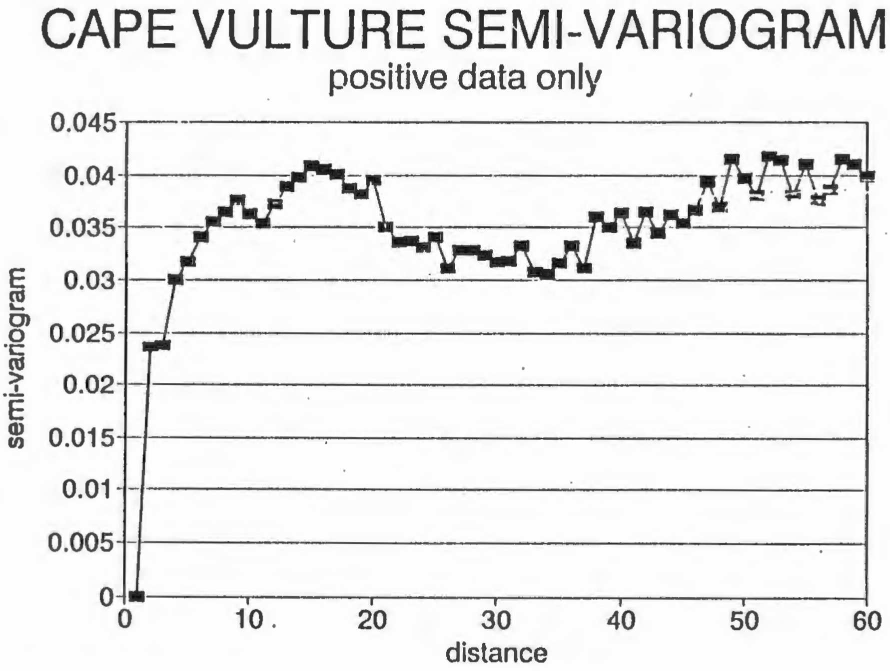


Figure 3.37 Semi-variogram using positive data and those grid-cells close to positive data (i.e. within 3 mm = 45 km on the ground). (Graphic drawn by L. McNeill.)

Both methods 2 and 3 involve some form of regional weighting which is based upon the assumption of spatial independence, i.e. the reporting rate in a given grid-cell is assumed to be independent of the reporting rates in the surrounding cells. But it is likely that the reporting rates in adjacent grid-cells are not independent and so consideration must be given to a method which allows binomial samples to be pooled while taking account of their spatial autocorrelation.

Method 4: Binomial Kriging.

Given that the reporting rate is a binomial variable it is tempting to want to use some adaptation of generalized linear models (GLM) to model its geographical variation. However, the direct use of GLM is not possible, as McCullagh and Nelder (1989: p.21) state:

> An important characteristic of generalized linear models is that they assume independent (or at least uncorrelated) observations. ... As a consequence, data exhibiting the autocorrelations of time series and spatial processes are expressly excluded.

At the request of the SABAP management (L.G. Underhill pers. comm.) the problem of smoothing the reporting rate in a statistically acceptable form was investigated by W.L. Zucchini and colleagues in the Statistical Sciences Department, University of Cape Town. A solution has been proposed (McNeill 1991) which takes care of the spatial autocorrelation, via kriging, in the binomial GLM.

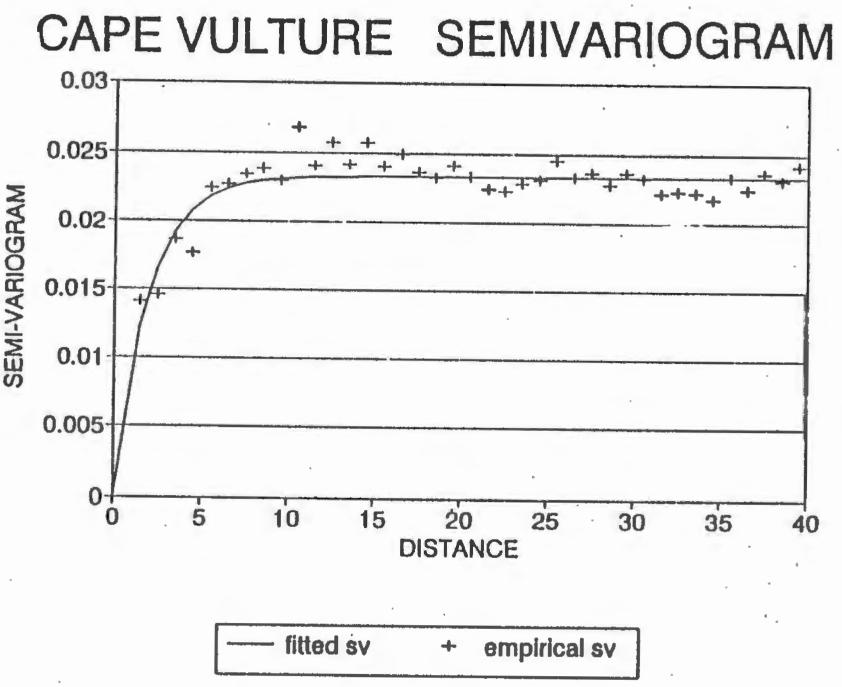


Figure 3.38 Modelling the semi-variogram using the exponential function. (Graphic drawn by L. McNeill.)

> The technique of kriging is commonly used to obtain a best linear unbiased predictor of a spatially correlated random variable. ... When the variance of the measurement error is known, the kriging equations are readily adjusted to provide the optimum *measurement error-free* predictor. ... For binomial data, the measurement error is dependent on both the true probability and the sample size. It can, however, be estimated from the data. (McNeill 1991: 131; author's italics).

The SABAP data for the Cape Vulture were tidied up and given to L. McNeill for analysis. The following results come directly from the application of the technique described below.

A semi-variogram was constructed using all the data (Figure 3.36), including grid-cells in which there were no sightings of Cape Vulture. This was discarded because of the danger of using negative evidence - how can it be distinguished from missing data? Using only those grid-cells in which Cape Vultures were present, or were close to grid-cells with Cape Vulture sightings, a new semi-variogram was constructed (Figure 3.37). It is seen that this flattens after about 7 mm (at map scale = 105 km on the ground). This was fitted with a theoretical semi-variogram of an exponential form (Figure 3.38). Using this empirical model the grid-cells were taken one at a time and using all other grid-cells within 5 mm (i.e. 75 km on the ground) an estimate was made of the reporting rate in that neigbourhood. These estimates were used to construct a contour map (Figure 3.39) in which the 2%, 3%, 4% and 5% reporting rate contours are shown.

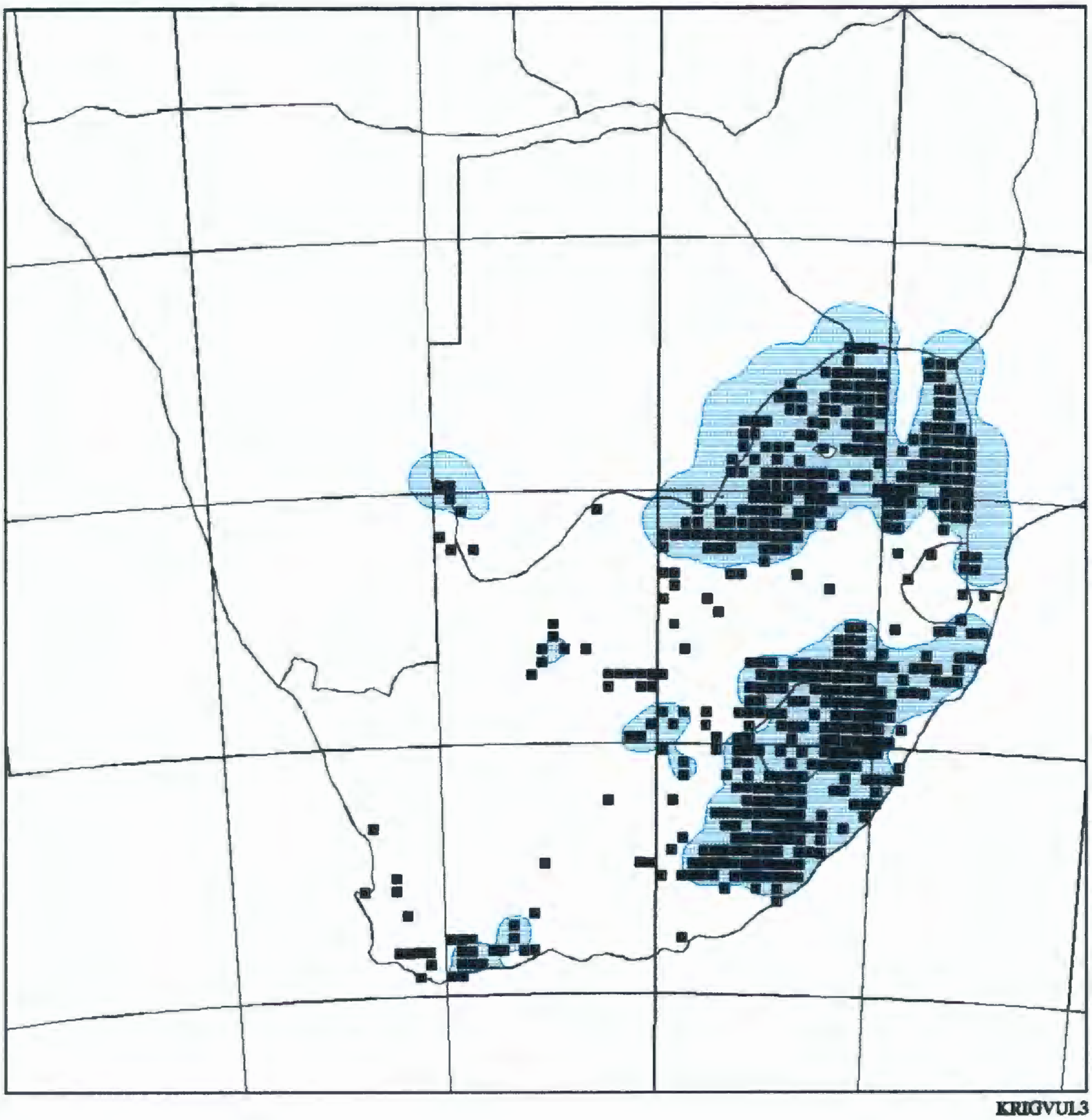


Figure 3.40 The 3% contour from the reporting rate data smoothed using kriging is chosen to represent the current distribution of the Cape Vulture. Note that no SABAP field cards for Namibia, Botswana or Zimbabwe were available for inclusion.

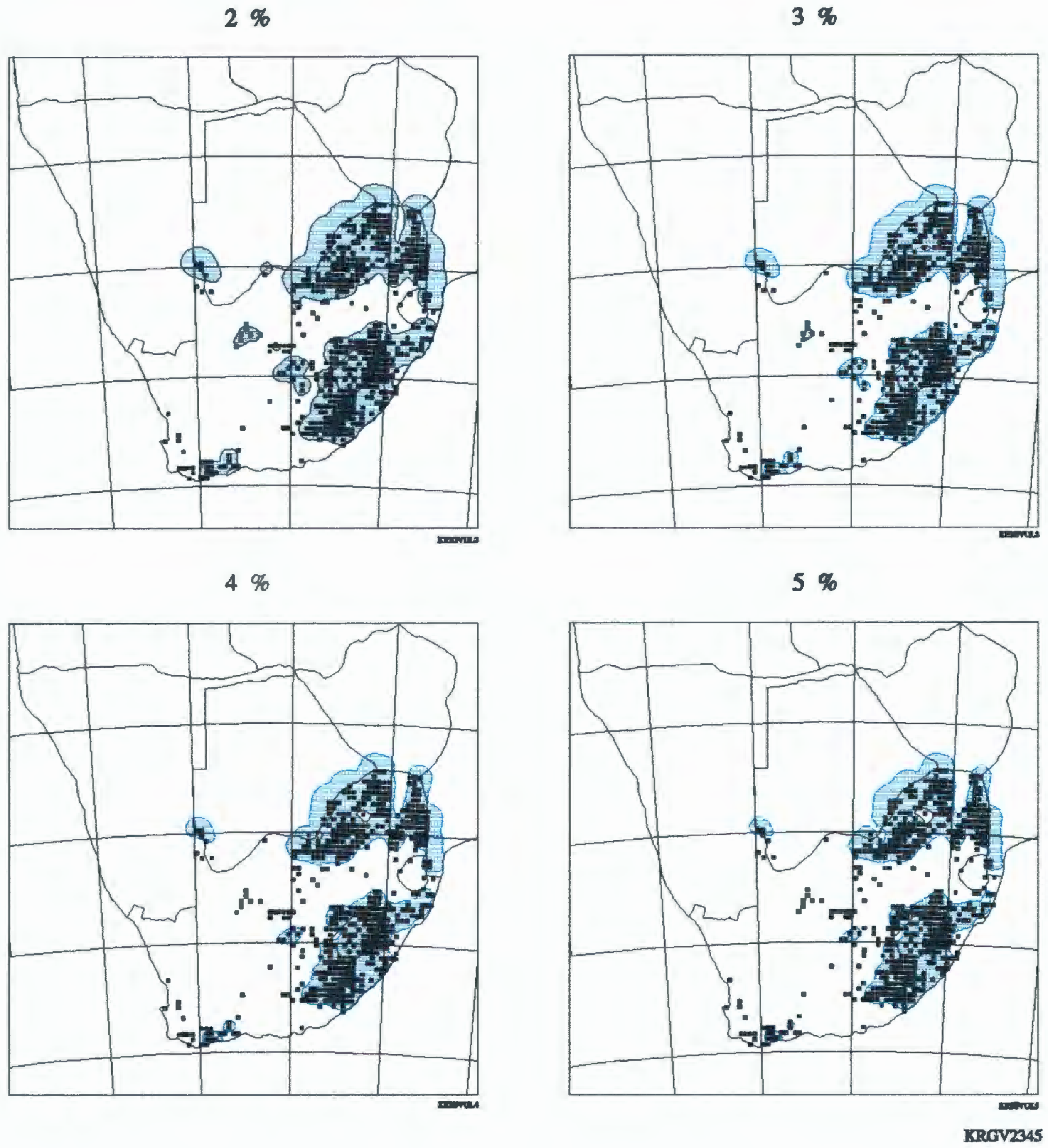


Figure 3.39 Cape Vulture reporting rate smoothed using binomial kriging. Grid-cells with Cape Vultures present are shown as black dots and are compared with four reporting rate contours. A. 2%. B. 3%. C. 4% D. 5%.

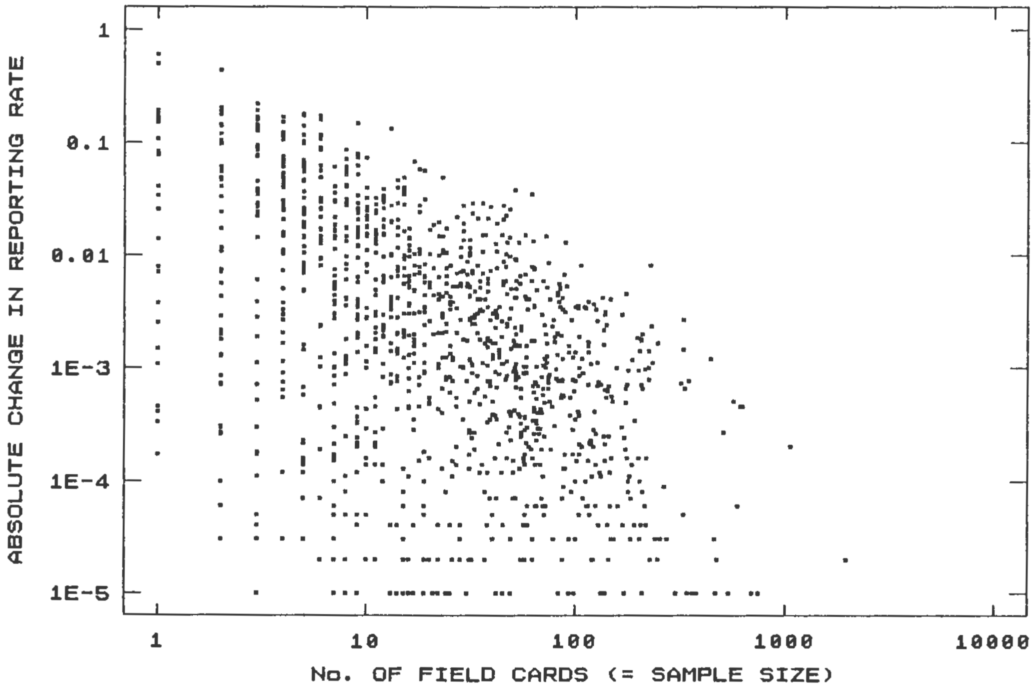


Figure 3.41 Absolute difference between the observed and estimated reporting rate as a function of sample size, N = 1446.

An estimate of reporting rate was provided for 1446 grid-cells: 512 with at least one observation of reporting rate and 934 close to positive cells. The difference between the estimated reporting rate (i.e. the 'kriged' value) and the observed reporting rate was computed for each of these 1446 cells and it is seen that the absolute difference decreases rapidly as the sample size (= number of field cards) increases (Figure 3.41). This is a desirable property because the reporting rates observed in grid-cells with large samples are well estimated and so should not be changed by any appreciable amount. For 10 or more cards the reporting rate is changed by less than about 0.1 while for sample sizes of at least 100 the change is less than 0.01. Another way of seeing this phenomenon is to look at the variation of the standard error of the kriged reporting rate as a function of sample size (Figure 3.42). This too is seen to decrease strongly with sample size. Its maximum value is just over 0.1 for small samples and decreases to about 0.02 for at least 100 field cards.

Summary

Which of the spatial distributions mapped in this section can be said to yield the definitive 'distribution of the Cape Vulture'? Obviously none of them. It all depends on the objectives of the mapping process. It is suggested on the grounds of common sense alone that a good distribution map should satisfy two broad criteria:

1) It should include most of the sightings, excepting the spatial outliers.
2) It should be a broadly smoothed map showing the major geographical patterns.

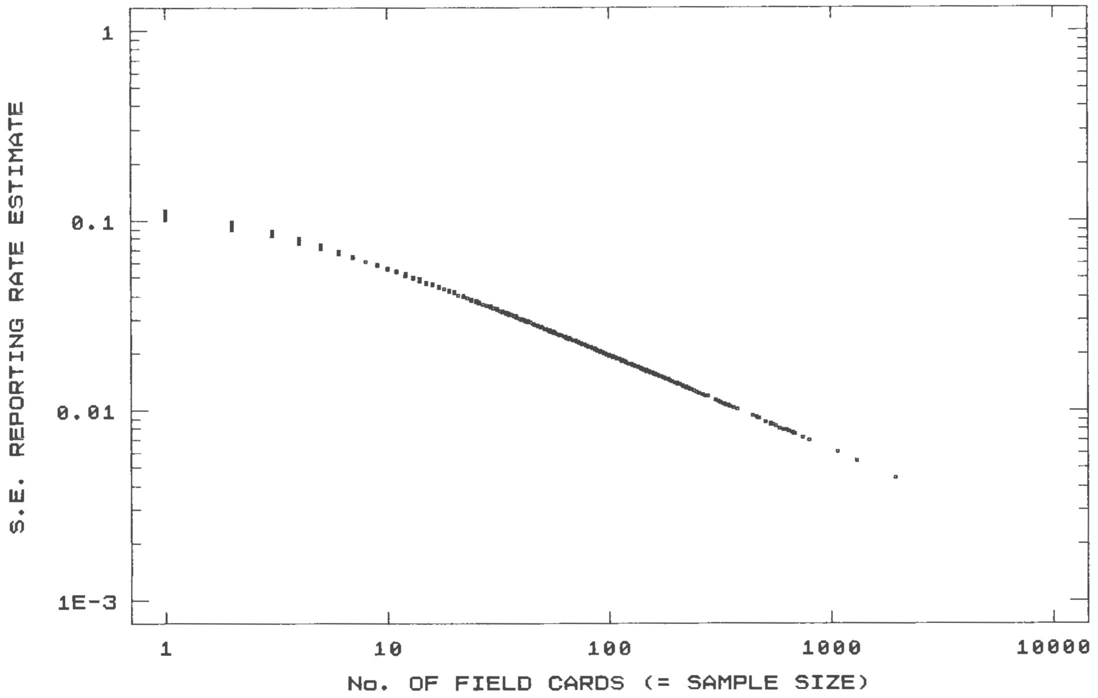


Figure 3.42 Standard error of the kriged estimate of the reporting rate as a function of sample size, N = 1446.

After some experimentation it is suggested that a map which is based on a reporting rate of 3% will satisfy both these criteria (Figures 3.39 C and .40). From an examination of this map it is seen that the major 'heartlands' of the Cape Vulture are:

1) The western, northern and eastern Transvaal.
2) The eastern Cape, Transkei, most of Lesotho, most of Natal but excluding the central coastal zone, southeast and southwest O.F.S.

There are minor 'pockets' of Cape Vultures in the following regions.

1) Southwestern Cape.
2) Karoo and northern Cape , two pockets.
3) Kalahari Gemsbok National Park.

The major areas of omission, relative to maps in most fields guides are as follows.

1) A major 'pie-shaped' piece in the northern Transvaal.
2) Most of the southern Transvaal, most of the O.F.S., some of Natal and most of the Cape.

The relationship between the distributions elucidated from the SABAP sightings data will be compared with those deduced from the colony and roost data below (see section 3.2.11).[1]

---

[1] Two examiners wanted further information on Kriging (including semi-variograms) as a technique for the spatial interpolation of a binomial variable (i.e. the reporting rate). The technique is fully explained and illustrated using SABAP data by McNeill (1991) to whom reference should be made.

Exhibit 3.2.5.1

Computation of the smoothed reporting rate

Program stored on F: \MCAD \REPRATE2.MCD

Set the origin of matrices and vectors $\mathrm{ORIGIN} \equiv 1$

Number of columns in data matrices $\mathrm{Imax} := 96$

Number of rows in data matrices $\mathrm{Jmax} := 80$

Read in the number of Cape Vulture sightings

$i := 1 .. \mathrm{Imax}$

$j := 1 .. \mathrm{Jmax}$

$CV_{(i,j)} := \mathrm{READ}\left[\mathrm{SPPTOT}_{\mathrm{PRN}}\right]$

Read in the number of Check Lists

$i := 1 .. \mathrm{Imax}$

$j := 1 .. \mathrm{Jmax}$

$\mathrm{Lists}_{(i,j)} := \mathrm{READ}\left[\mathrm{FLDTOT}_{\mathrm{PRN}}\right]$

Set the mask size for smoothing $\mathrm{Mask} := 3$

Create a mask with centre-weighting

$$w := \begin{bmatrix} 1 & 2 & 1 \\ 2 & 4 & 2 \\ 1 & 2 & 1 \end{bmatrix}$$

Compute the offset for the mask $\mathrm{Offset} := \mathrm{floor}\left[\dfrac{\mathrm{Mask}}{2}\right] + 1$

$\mathrm{Offset} = 2$

Initialise the accumulation matrix
for the number of Cape Vulture sightings

$i := 1 .. \mathrm{Imax}$

$j := 1 .. \mathrm{Jmax}$

$md_{(i,j)} := 0$

Initialise the accumulation matrix
for the number of Check Lists

$i := 1 .. \mathrm{Imax}$

$j := 1 .. \mathrm{Jmax}$

$Md_{(i,j)} := 0$

Initialise the reporting rate matrix

$i := 1 .. \mathrm{Imax}$

$j := 1 .. \mathrm{Jmax}$

$R_{(i,j)} := 0$

Exhibit 3.2.5.1 (Continued)

Count the number of Cape Vulture sightings 'under the mask'

$i := \text{Offset} .. \text{Imax} - \text{Offset} + 1$

$j := \text{Offset} .. \text{Jmax} - \text{Offset} + 1$

$k := 1 .. \text{Mask}$

$l := 1 .. \text{Mask}$

$$md_{(i,j)} := \sum_{k} \sum_{l} CV_{(i+k-\text{Offset},\, j+l-\text{Offset})} \cdot w_{(k,l)}$$

Count the number of Check Lists 'under the mask'

$i := 1 + \text{Offset} .. \text{Imax} - \text{Offset}$

$j := 1 + \text{Offset} .. \text{Jmax} - \text{Offset}$

$k := 1 .. \text{Mask}$

$l := 1 .. \text{Mask}$

$$Md_{(i,j)} := \sum_{k} \sum_{l} \text{Lists}_{(i+k-\text{Offset},\, j+l-\text{Offset})} \cdot w_{(k,l)}$$

Compute the smoothed reporting rate

$i := 1 .. \text{Imax}$

$j := 1 .. \text{Jmax}$

$$R_{(i,j)} := \text{if}\left[Md_{(i,j)} > 0, \frac{md_{(i,j)}}{Md_{(i,j)}}, 0 \right]$$

Remember to trap division by zero

Write out the reporting rate

$i := 1 .. \text{Imax}$

$j := 1 .. \text{Jmax}$

$$\text{OutRepRate}_{(\text{Jmax} \cdot i - \text{Jmax} + j)} := R_{(i,j)}$$

$k := 1 .. \text{Imax} \cdot \text{Jmax}$

$$\text{WRITE}\left[\text{R3cent} \right] := \text{OutRepRate}_{k}$$

Exhibit 3.2.5.2

Computation of a weight matrix based on a radially symmetric bivariate normal distribution

Stored on F: \MCAD \NORMW.MCD

Standard deviation measured in pixels

$s := 2.2$

Define the origin

$x := 0$

$y := 0$

$i := 0 \,..\, 4$

$j := 0 \,..\, 4$

Bivariate normal distribution centred on the origin

$$f(x, y) := \left[\frac{\exp\left[\frac{-\left[x^2 + y^2 \right]}{\left[2 \cdot s^2 \right]} \right]}{\left[2 \cdot p \cdot s^2 \right]} \right]$$

Compute the lower right quarter of the weight matrix

$$w_{(i+4,\, j+4)} := \int_{i-\frac{1}{2}}^{i+\frac{1}{2}} \int_{j-\frac{1}{2}}^{j+\frac{1}{2}} f(x, y)\, dy\, dx$$

Fill in the lower left quadrant of the matrix

$i := 0 \,..\, 4$

$j := 4 \,..\, 8$

$$w_{(i,\, j)} := w_{(8-i,\, j)}$$

Fill in the top half of the matrix

$i := 0 \,..\, 8$

$j := 0 \,..\, 4$

$$w_{(i,\, j)} := w_{(i,\, 8-j)}$$

$i := 0 \,..\, 8 \quad j := 0 \,..\, 8$

$$\sum_i \sum_j w_{(i,\, j)} = 0.92$$

Compute the sum of the weights - they should be almost unity

Write out matrix

WRITEPRN (WMAT) := w

$$w = \begin{bmatrix} 0.001 & 0.003 & 0.004 & 0.006 & 0.006 & 0.006 & 0.004 & 0.003 & 0.001 \\ 0.003 & 0.005 & 0.009 & 0.012 & 0.013 & 0.012 & 0.009 & 0.005 & 0.003 \\ 0.004 & 0.009 & 0.014 & 0.019 & 0.022 & 0.019 & 0.014 & 0.009 & 0.004 \\ 0.006 & 0.012 & 0.019 & 0.026 & 0.029 & 0.026 & 0.019 & 0.012 & 0.006 \\ 0.006 & 0.013 & 0.022 & 0.029 & 0.032 & 0.029 & 0.022 & 0.013 & 0.006 \\ 0.006 & 0.012 & 0.019 & 0.026 & 0.029 & 0.026 & 0.019 & 0.012 & 0.006 \\ 0.004 & 0.009 & 0.014 & 0.019 & 0.022 & 0.019 & 0.014 & 0.009 & 0.004 \\ 0.003 & 0.005 & 0.009 & 0.012 & 0.013 & 0.012 & 0.009 & 0.005 & 0.003 \\ 0.001 & 0.003 & 0.004 & 0.006 & 0.006 & 0.006 & 0.004 & 0.003 & 0.001 \end{bmatrix}$$

3.2.6 What is a distribution map?

In previous sections examples of Cape Vulture distribution maps have been compared with those resulting from mapping 1) population densities, 2) presence and absence and 3) reporting rates. Before proceeding, it is worthwhile to stop and consider the question: 'what is a distribution map'? What does a species' distribution map portray?

It is instructive to examine the explanations given in some of the southern African avian field-guides and handbooks. The distribution map (Newman 1988: 15):

> [shows] ... the areas in which it is likely to be found ... These ranges are rough guides only, based on present-day knowledge of the bird's occurrence ... local ranges of isolated populations ... where a species has been recorded but is not regular.

A more circumspect approach is taken by Maclean (1985: xxxiv-xxxv):

> maps designed as a rough guide to the area over which a particular species can most likely be found. Birds are dynamic organisms and not confined to rigid boundaries as a rule; nor do they necessarily occur uniformly throughout ... since there must inevitably be larger or smaller areas of unsuitable habitat ... maps must be treated with caution

In describing species distributions the following terms are often used: resident, rare, migrant, vagrant, extralimital, etc. What do these terms mean and can they be quantified? It has been suggested (Maclean 1985: xxxiv):

> Terms relating to abundance are necessarily somewhat arbitrary ... A species that is very plentiful in an area, and likely to be seen every day in considerable numbers will fall into the category "abundant" or "very common" ... Decreasing degrees of abundance are described by expressions like common, fairly common, uncommon, scarce (or sparse), rare or very rare. They do not necessarily correspond with any accurately measurable numerical value, though they could often be made to do so; such a situation, however, is rather artificial and expressions of abundance are intended only to give a reasonable subjective idea of how readily one may see a species in a given area.

A less cautious approach has been adopted by Newman (1988: 18) who gives the following definitions:

Newman Category	*Definition*
Vagrant	Species not normally seen in southern Africa
Rare	Species recorded 10 times or less in any year in suitable habitat
Uncommon	Species recorded 30 or less times in a month in suitable habitat
Fairly common	Species recorded 1-10 times a day in suitable habitat
Common	Species recorded 10-50 times a day in suitable habitat
Very common	Species recorded 50-100 times a day in suitable habitat
Abundant	Species recorded 100+ times a day in suitable habitat
Resident	Species which breeds in southern Africa

An expansive view of what a distribution map should do has been made for vultures (Mundy, Butchart, Ledger & Piper 1982: 26):

> A good distribution map should portray the *status* of a species as well as its range. The status attempts to answer three questions. Where does a species breed, where does it occur commonly, and where is it only as a vagrant? Where do large numbers occur, either breeding or simply present, and are these

> places constant? And is the species increasing, stable, or decreasing? These answers would give texture, volume, and movement to a distribution map - to our knowledge, no such global map exists for any species of vulture (except the California Condor where the map now reads virtually zero).

The problem of 'currency' has been described for Red Data Books, and it also applies to published species distribution maps (Hall 1989: 150):

> has its information fixed the moment it appears in print. It can record only a snapshot view of a dynamic situation ... The professional conservationist prefers to obtain the latest information directly from ... a regularly revised data-bank.

Most species distribution maps tend to show the distribution for all of recorded history (see Cape Vulture maps in Maclean 1985: 109 and Snow 1978: 66). Manual systems are too difficult to update: this leads immediately to the suggestion (Hall 1989: 151) that the best distribution maps are those in a geographic information system.

Until recently, distribution maps for resident species did not distinguish between the breeding distribution and the species' range but it is likely that these may differ markedly. To gain clarity on this issue, and others raised in the next four sections, a brief review of modern animal mapping schemes has been undertaken. This review includes most southern African animal atlases as well as a selection from elsewhere in the world, specialist mapping schemes and examples of field guides. Data were collected under the following headings:

Source: Author and date.
Bibliographic details.

Taxon: Taxonomic group.

Region: Continent, subcontinent, country or province.

Period: Start of major data collection, to nearest year.
End of data collection, to nearest year.

Sources: Fields cards (= check lists), were they used to collect data?
Single species records, were they included in the mapping process?
Ringing data, were they included in the mapping process?
Oological records, were they included in the mapping process?
Museum specimens, were they included in the mapping process?
Latitude & longitude grid. Were the data recorded on a grid using geographical latitude and longitude? If so, to what grid size?
¼° by ¼° grid-cell.
½° by ½° grid-cell.
1° by 1° grid-cell.
Larger grid-cell.
Graticule grid-cell. Was a grid, based on a standard map, used for geo-referencing? If so, to what grid size?
10 km by 10 km.
Breeding data. Were these collected simultaneously?
Counts. Were the numbers of birds, of each species seen recorded?

Analyses:
- Spatial.
- Seasonal.
- Temporal (i.e. longer than a year).
- Sympatry, allopatry, etc.
- Use of spatial statistics.
- Use of a geographic information system.

Presentation:
- Individual records.
    - Symbols.
- Presence and absence.
- Raw reporting rate.
    - Same metric for all species.
    - Species-specific metric.
- Smoothed reporting rate.
- Use of colour.
    - Blue.
    - Red.

The summaries of the literature reviewed are shown in the four tables that follow and are discussed in the next four sections of this chapter. Examples of the sorts of questions that should be asked of distribution maps are:

1) Where is a given species to be seen? How likely is it that it will be seen there; on 10%, 1%, 0.1% or 0.01% of visits?
2) Was the sighting of a rare species acceptable to the local Rare Bird Committee?
3) Where can a given species currently be seen?
4) How will the distribution of a species change with season and time?

3.2.7 What can be portrayed on a distribution map?

A variety of spatially varying data-sets have been generated for the Cape Vulture in these researches. Consideration must now be given to the ways in which they may be portrayed. To this end the review of animal atlases (see previous section) is examined. It is found that the following data-sets can be portrayed on a distribution map:

1) Individual records. Each record, or a subset of the records in a small region (e.g. specimen, sighting and breeding) may be displayed using a different symbol. For the Cape Vulture, distributional and breeding records are shown separately by Snow (1978: 66).
2) Presence and absence. An example using the Cape Vulture is the map in Mundy (1982: 80) where roosting sites, regular occurrences and sporadic occurrences are distinguished.

Table 3.20

Atlas projects and publications reviewed. Citation, taxon, region and mapping period.

No.	Reference	Taxon	Region	Start Atlas year	End Atlas Year
1	Abrams *et al.* 1981	Birds	Marine	N/A	N/A
2	Ash & Miskell 1983	Birds	Somalia	N/A	N/A
3	Borello 1987	Vultures	Botswana	1970	1987
4	Boshoff & Vernon 1980a	Vultures	Cape	1600	1978
5	Boshoff, Brooke & Crowe 1978	Vultures	southern Africa	1600	1977
6	Boshoff, Vernon & Brooke 1983	Raptors	Cape	1600	1980
7	Boshoff & Vernon 1980b	Raptors	Cape	1700	1980
8	Brown *et al.* 1982	Birds	Africa	N/A	N/A
9	Buckland, Bell & Picozzi 1990	Birds	Scotland	N/A	N/A
10	Busche & Staudte 1985	Birds	Germany	N/A	N/A
11	Curry-Lindahl 1981	Birds	Africa	N/A	N/A
12	Cyrus & Robson 1980	Birds	Natal	1970	1979
13	Davis 1989	Birds	Devon	N/A	N/A
14	Donázar *et al.* 1987	Raptors	northern Spain	N/A	N/A
15	Du Plessis 1986	Raptors	S.E. O.F.S.	N/A	N/A
16	Earlé & Grobler 1987	Birds	O.F.S.	1983	1986
17	Fuller & Lloyd 1981	Plovers	Britain	N/A	N/A
18	Hall & Moreau 1970	Birds	Africa	1700	1970
19	Harrison 1982	Birds	West Palearctic	N/A	N/A
20	Humphries & Parenti 1986	Birds	N/A	N/A	N/A
21	Inskipp & Inskipp 1985	Birds	Nepal	N/A	N/A
22	Laughlin *et al.* 1982	Birds	North America	N/A	N/A
23	Lewis & Pomeroy 1988	Birds	Kenya	N/A	N/A
24	Mundy 1982	Vultures	southern Africa	1973	1980
25	Nikolaus 1987	Birds	Sudan	1976	1984
26	Pomeroy & Lewis 1983	Birds	Kenya	N/A	N/A
27	Sharrock 1976	Birds	Britain	N/A	N/A
28	Snow 1978	Birds	Africa	1700	1976
29	Stuart *et al.* 1985	Predators	Cape	1700	1985
30	Tarboton 1968	Birds	S.E. Transvaal	N/A	N/A
31	Udvardy 1969	N/A	N/A	N/A	N/A
32	Utschick 1984	N/A	Germany	N/A	N/A
33	Walton 1984	N/A	southern Africa	N/A	N/A
34	Woods 1975	Birds	Falklands	N/A	N/A

Table 3.21

Atlas projects and publications reviewed. Data collected

		Sources					Spatial					Other			
No.	Reference	CHKL	SSPP	RING	EGG	MUSM	LATL	QART	HALF	ONE	BIGR	GRID	TEMK	BRED	NUMB
1	Abrams *et al.* 1981	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	Ash & Miskell 1983	Y	Y	-	-	Y	Y	-	Y	-	-	-	-	Y	-
3	Borello 1987	Y	Y	-	-	Y	Y	-	Y	-	-	-	-	Y	Y
4	Boshoff & Vernon 1980a	Y	Y	Y	Y	Y	Y	Y	-	-	-	-	-	Y	Y
5	Boshoff, Brooke & Crowe 1978	Y	Y	-	-	Y	Y	Y	-	-	-	-	-	Y	-
6	Boshoff, Vernon & Brooke 1983	Y	Y	Y	Y	Y	Y	Y	-	-	-	-	-	Y	-
7	Boshoff & Vernon 1980b	Y	Y	-	Y	Y	Y	Y	-	-	-	-	-	Y	-
8	Brown *et al.* 1982	-	Y	-	-	-	-	-	-	-	-	-	-	Y	-
9	Buckland, Bell & Picozzi 1990	Y	-	-	-	-	-	-	-	-	-	Y	Y	Y	-
10	Busche & Staudte 1985	-	Y	-	-	-	-	-	-	-	-	Y	-	-	-
11	Curry-Lindahl 1981	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12	Cyrus & Robson 1980	Y	Y	Y	Y	Y	Y	Y	-	-	-	-	-	Y	-
13	Davis 1989	-	-	-	-	-	-	-	-	-	-	-	-	-	-
14	Donázar *et al.* 1987	-	-	-	-	-	-	-	-	-	-	-	-	Y	-
15	Du Plessis 1986	-	-	-	-	-	Y	Y	-	-	-	-	-	Y	-
16	Earlé & Grobler 1987	Y	-	-	-	-	Y	Y	-	-	-	-	-	-	-
17	Fuller & Lloyd 1981	-	-	-	-	-	-	-	-	-	-	-	-	-	-
18	Hall & Moreau 1970	-	-	-	-	Y	Y	-	-	-	-	-	-	-	-
19	Harrison 1982	-	-	-	-	-	-	-	-	-	-	-	-	-	-
20	Humphries & Parenti 1986	-	-	-	-	-	-	-	-	-	-	-	-	-	-
21	Inskipp & Inskipp 1985	-	Y	-	-	-	-	-	-	-	-	-	-	Y	-
22	Laughlin *et al.* 1982	-	-	-	-	-	-	-	-	-	-	-	-	Y	-
23	Lewis & Pomeroy 1988	-	-	-	-	-	-	-	-	-	-	-	-	-	-
24	Mundy 1982	Y	Y	Y	Y	Y	Y	-	-	-	-	-	-	Y	Y
25	Nikolaus 1987	Y	Y	-	-	-	-	-	-	Y	-	-	-	Y	-
26	Pomeroy & Lewis 1983	-	-	-	-	-	-	-	-	-	-	-	-	-	-
27	Sharrock 1976	Y	-	-	-	-	-	-	-	-	-	Y	Y	Y	-
28	Snow 1978	-	-	-	-	Y	Y	-	-	-	-	-	-	Y	-
29	Stuart *et al.* 1985	-	Y	-	-	Y	Y	-	-	-	-	-	-	-	-
30	Tarboton 1968	Y	Y	Y	-	-	Y	-	-	-	-	-	-	Y	-
31	Udvardy 1969	-	-	-	-	-	-	-	-	-	-	-	-	-	-
32	Utschick 1984	-	-	-	-	-	-	-	-	-	-	Y	-	-	-
33	Walton 1984	-	-	-	-	-	-	-	-	-	-	-	-	-	-
34	Woods 1975	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Notes: The following column headings are used:

CHKL.	Were species' check-lists (= field cards) used?
SSPP.	Were single species' records admitted?
RING.	Were ringing data admitted?
EGG.	Were egg-collectors' data admitted?
MUSM.	Were museum specimens admitted ?
LATL.	Were the data recorded on a latitude & longitude grid?

QART. Were the data recorded to within a ¼° by ¼° grid-cell?
HALF. Were the data recorded to within a ½° by ½° grid-cell?
ONE. Were the data recorded to within a 1° by 1° grid-cell?
BIGR. Were the data recorded to within a bigger grid-cell?
GRID. Were the data recorded to rectangular area on a map?
TEMK. Was a 10 by 10 km grid used?
BRED. Were breeding data collected?
NUMB. Were the numbers of different birds of each species counted?

Table 3.22

Atlas projects and publications reviewed. Analyses performed.

No.	Reference	Spatial analysis?	Season analysis?	Trend analysis?	Anlysis of Sympatry	Use of Spatial Stats?	Use of a GIS?
1	Abrams *et al.* 1981	Y	-	-	-	-	-
2	Ash & Miskell 1983	Y	-	-	-	-	-
3	Borello 1987	Y	-	-	-	-	-
4	Boshoff & Vernon 1980a	Y	-	Y	-	-	-
5	Boshoff, Brooke & Crowe 1978	Y	-	-	-	-	-
6	Boshoff, Vernon & Brooke 1983	Y	-	-	-	-	-
7	Boshoff & Vernon 1980b	Y	-	-	-	-	-
8	Brown *et al.* 1982	-	-	-	-	-	-
9	Buckland, Bell & Picozzi 1990	Y	Y	-	-	Y	-
10	Busche & Staudte 1985	Y	-	-	-	-	-
11	Curry-Lindahl 1981	-	Y	Y	-	-	-
12	Cyrus & Robson 1980	-	Y	-	Y	-	-
13	Davis 1989	-	-	-	-	-	-
14	Donázar *et al.* 1987	Y	-	-	-	-	-
15	Du Plessis 1986	Y	-	Y	-	-	-
16	Earlé & Grobler 1987	-	Y	-	-	-	-
17	Fuller & Lloyd 1981	-	-	-	-	-	-
18	Hall & Moreau 1970	Y	-	-	Y	-	-
19	Harrison 1982	-	-	-	-	-	-
20	Humphries & Parenti 1986	-	-	-	-	-	-
21	Inskipp & Inskipp 1985	-	-	-	-	-	-
22	Laughlin *et al.* 1982	-	-	-	-	-	-
23	Lewis & Pomeroy 1988	-	-	-	-	-	-
24	Mundy 1982	Y	Y	Y	Y	-	-
25	Nikolaus 1987	-	-	-	-	-	-
26	Pomeroy & Lewis 1983	-	-	-	-	Y	-
27	Sharrock 1976	-	-	-	-	-	-
28	Snow 1978	-	-	-	Y	-	-
29	Stuart *et al.* 1985	Y	-	-	-	-	-
30	Tarboton 1968	-	-	-	-	-	-
31	Udvardy 1969	-	-	-	-	-	-
32	Utschick 1984	Y	-	-	-	-	-
33	Walton 1984	-	-	-	-	-	-
34	Woods 1975	-	-	-	-	-	-

Table 3.23

Atlas projects and publications reviewed. Presentation.

		Individual records		Seasonal Spatial						Colour				Additional			
No.	Reference	INDR	SYMB	PRES	RREP	CREP	SREP	ROSE	HIST	COLR	BLUE	RED	GAZ	LOCL	SCAL	MAPP	OVER
1	Abrams *et al.* 1981	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	Ash & Miskell 1983	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	Borello 1987	-	-	Y	-	-	-	-	-	-	-	-	-	-	-	-	-
4	Boshoff & Vernon 1980a	-	-	Y	-	-	-	-	-	-	-	-	Y	-	-	-	-
5	Boshoff, Brooke & Crowe 1978	-	-	Y	-	-	-	-	-	-	-	-	-	-	-	-	-
6	Boshoff, Vernon & Brooke 1983	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7	Boshoff & Vernon 1980b	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8	Brown *et al.* 1982	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9	Buckland, Bell & Picozzi 1990	-	-	-	Y	-	-	-	-	Y	-	Y	-	-	-	-	-
10	Busche & Staudte 1985	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11	Curry-Lindahl 1981	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12	Cyrus & Robson 1980	-	-	Y	-	-	-	-	-	-	-	-	-	-	-	-	Y
13	Davis 1989	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
14	Donázar *et al.* 1987	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
15	Du Plessis 1986	-	-	Y	-	-	-	-	-	-	-	-	-	-	-	-	-
16	Earlé & Grobler 1987	-	-	Y	-	-	-	Y	-	-	Y	-	-	-	-	-	-
17	Fuller & Lloyd 1981	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
18	Hall & Moreau 1970	Y	Y	-	-	-	-	-	-	-	-	-	-	-	-	-	-
19	Harrison 1982	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
20	Humphries & Parenti 1986	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
21	Inskipp & Inskipp 1985	-	Y	Y	-	-	-	-	-	-	-	-	-	-	-	-	-
22	Laughlin *et al.* 1982	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
23	Lewis & Pomeroy 1988	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Y
24	Mundy 1982	Y	Y	-	-	-	-	-	-	-	-	-	-	-	-	-	-
25	Nikolaus 1987	Y	-	-	-	-	-	-	-	-	-	-	Y	-	-	-	-
26	Pomeroy & Lewis 1983	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
27	Sharrock 1976	-	-	Y	-	-	-	-	-	-	-	-	-	-	-	-	Y
28	Snow 1978	Y	Y	-	-	-	-	-	-	-	-	-	-	-	-	-	-
29	Stuart *et al.* 1985	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
30	Tarboton 1968	-	-	Y	-	-	-	-	-	-	-	-	-	-	-	-	-
31	Udvardy 1969	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
32	Utschick 1984	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
33	Walton 1984	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
34	Woods 1975	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Notes: The following column headings are used:
INDR. Were individual records plotted?
SYMB. Were different symbols used to plot different types of individual records?
PRES. Were the distributional data plotted as presence or absence only?
RREP. Was the raw reporting rate used to portray relative density?
CREP. Was a constant scale used to portray all reporting rates?

SREP. Was a separate reporting rate used for each species' distribution map?
ROSE. Was a rose used to portray seasonal variations?
HIST. Was one, or more, histograms used to portray seasonal variations?
COLR. Was colour used on the map (i.e. as opposed to black and white only)?
BLUE. Were distributions plotted using blue?
RED. Were distributions plotted using red?
GAZ. Was a gazetteer supplied?
LOCL. Was a locality map given?
SCAL. Was the locality map given at the same scale as the distribution maps?
MAPP. Was the map projection stated?
OVER. Were transparent overlays provided?

3) Multiple presence and absence. The method of presentation uses a single symbol with three forms, absent implies no record for the species, a hollow symbol implies presence while a filled symbol indicates positive evidence for breeding. An example of this, for the Cape Vulture may be found in Tarboton, Kemp & Kemp (1987: 42).
4) Reporting rate. The reporting rate can be shown in a number of different forms. An example for the Cape Vulture may be found in Hockey, Underhill, Neatherway & Ryan (1989: 35) where the reporting rate is represented by a circle whose radius is proportional to the reporting rate.
5) Seasonality. This can be shown for each grid-cell, a group of grid-cells or the entire region. The commonest method used to date for the Cape Vulture is a twelve-leaf rose as may be seen in Cyrus & Robson (1980: 62) and Earlé & Grobler (1987: 75).
6) Breeding. Breeding can be shown on its own or in combination with one or more spatial and temporal attributes of the species. A Cape Vulture example may be found in Tarboton, Kemp & Kemp (1987: 42).

Without presenting extensive arguments, it is apparent, given a large number of adequate and uniform field cards, that the use of the reporting rate (or some function of it) is by far and away the best method of showing the Cape Vulture's distribution (see section 3.2.5 above). Unfortunately, the coverage in southern Africa is not uniform and is often particularly sparse in those country areas where Cape Vultures are likely to be found. Hence, it would be an advantage if single species' records could also be used. A single species' record is a once-off sighting and for the Cape Vulture there are three sources of once-off sightings.

1) Birds seen circling low over the countryside.
2) Vultures feeding at carcasses.
3) Birds loafing on low, temporary roosts (e.g. cliffs and power pylons).

Many such once-off records are reported directly to Vulture Study Group members, while others are submitted to bird club news-sheets. They usually come from motorists. It is my personal experience that there is a constant flow of such records, especially from the Transkei and that these show a higher density than is revealed from the Transkei field cards.

Because of the highly clumped nature of breeding sites in the Cape Vulture it is not feasible to use field card data, nor is it reasonable to use presence and absence maps with filled symbols to display breeding data (see section 3.2.10 below).

Thus, using techniques explored and used to date it is possible to display the species' range, reporting rate and breeding sites on maps as found in bird-atlases. However, no systematic method to display a mass of once-off records has been been developed.

3.2.8 Cartographic considerations for avian maps

An avian map is much like any other map. It must be clear and it must convey the spatial information in a form that the reader can readily comprehend. In designing maps to display geographical and other information about the Cape Vulture, the following points need to be borne in mind:

1) The map should be drawn on a recognized map projection and should, if possible, be at a standard scale. The details of the projection and scale should be readily available to the user. Almost without exception, distribution atlases do not give the map projection, some give the scale and less than half provide a scale-bar.
2) The symbols used must be easily comprehended and should be familiar to the user and should be used in conformity with current practice. Failure to do so may confuse the user, or even worse, convey the wrong information.
3) There should be sufficient cartographic detail on the map for the user to locate a particular point of interest and for users to be able to orient themselves.
4) The number of data-sets simultaneously portrayed on the map should be restricted to ensure that the design is simple and easy to assimilate. 'Cluttering' of spatial data is to be avoided as subtleties in the data can easily be lost in the visual confusion; as Harrison (1991: 95) has opined:

   > The proliferation of symbols on ... maps militates against the clarity and directness of communication which would otherwise be achieved. The tendency to cram as much information as possible into the maps produced in many bird atlases is counter-productive because it is hard to visualize any of the component classes of information and visualization is the reason for producing a map in the first place.

The use of a rose to display seasonal data leads to such cluttering and 'data-overload', in my opinion, that it is impossible to interpret the spatial patterns (see Cyrus & Robson 1980; Earlé & Grobler 1987).

5) The map should be on a map projection and at a scale that make it easy to transfer distributions, manually, to and from other maps used by other members of the scientific community working in the same region. Many users of species' distribution maps want to ask questions such as 'why is that there?' and to do so they need to be able to compare two or more distributions. This can easily be achieved if the data are mapped on the same projection and are at simple integer ratios of their scales. Examples of the excellent use of such standardization may be found in the clear plastic overlays containing environmental details and supplied with the avian atlases of Blakers, Davies & Reilly (1984), Cyrus & Robson (1980) as well as Sharrock (1976). The overlays from Sharrock (1976) can also be used with Lack (1986).

Distribution maps are sometimes seen as the natural end-product of an atlas project but they are also the starting point for studies in biogeography and conservation. Thus it is important that it should be possible to extract data and information from a map in addition to using it merely as a tool for portraying status.

3.2.9 Techniques for designing and constructing distribution maps

In my opinion, the best method of portraying a spatial data-set is dependent on both the nature of the data-set and the principle aim of the cartographer. Different methods of portrayal are reviewed here and evaluated; this includes considerations of both design and physical execution.

Individual records

An 'individual record' or 'single species record' is a record of one species at a given point in space and time; i.e. it is not from a bird-watcher's field card. Examples are sight records, breeding (or nest) records, museum skins and eggs. There is a tendency to plot different classes of individual record, of the same species, on a single map. For such multi-class maps different symbols can be used for each type of record, e.g. a triangle for a museum specimen, square for breeding and so on; see Snow (1978: 66) for an example using four different symbols to distinguish breeding and other records in two griffons (*Gyps coprotheres* and *G. rueppellii*). There are other examples of the use of this technique (loc. cit.: 225) with up to nine different symbols. But this technique does not work well if the symbols are too dense on the page. There should be little or no spatial overlap between the different symbol sets as this makes for 'cluttered' cartography.

Presence and absence maps

A presence and absence map is a binary approximation to a species' distribution without any suggestion of density of 'sightability'. These maps may be portrayed in two ways:

1) The first choice is between having a continuous zone showing the region in which the species is present. Continuous zones are favoured for small scale maps (typically 1 in $50*10^6$, or less) showing continent-wide distributions. For the Cape Vulture see examples in Maclean (1985: 109) and Steyn (1982: 22). These binary maps are easily constructed as a black region on a white background and are readily extended to indicate summer and winter distributions by the use of hatching or multiple colours; see Cramp & Simmons (1980: 74-75) for the summer and winter distribution of the Eurasian Griffon *G. fulvus*.
2) The presence or absence of a record in an individual grid-cell may be shown by means of a symbol. The commonest symbol is a circle which may be either hollow or filled so as to convey some secondary information such as breeding; see Mundy (1982: 80), Tarboton & Allan (1984: 15) and Tarboton, Kemp & Kemp (1987: 42) for Cape Vulture examples.

Reporting rate

The use of the reporting rate is one level more complex than a binary presence and absence map in that it has a third dimension (i.e. a rate) to portray in addition to the two components of the spatial dimension. The following methods may be used to portray the reporting rate:

1) A discrete symbol per grid-cell (e.g. a circle or triangle) with either the size or area proportional to the reporting rate, e.g. Lack (1986) and Sharrock (1976). The symbol can be left empty or filled in order to convey some other spatial information, e.g. breeding; see the excellent examples in the Australian atlas (Blakers, Davies & Reilly 1984).
2) A filled-in grid-cell in which the area-fill has a grey-scale related to the reporting rate via some monotonic look-up table; see Harrison (1991: 110). The grey-scale can be replaced with pseudo-colour in which the range of reporting rates from low to high are represented by pure colours ranging from short to long wavelengths.
3) A contour-map in which the individual reporting rates have been smoothed and interpolated to give a set of reasonably 'clean' contours. These contours may be annotated with the reporting-rate values, have various thicknesses to indicate increasing values or be colour-coded.
4) Smoothed density shading, continuous symbols or colour-zones may also be used.
5) Three-dimensional views or projections are often favoured for 'gee-whiz' presentations.

Seasonal variations

Seasonal variations in both sightings and breeding are often displayed. The most frequently used techniques used are:

1) Twelve-leaf rose. Used in a number of atlases and without doubt a cartographic disaster; see Cyrus & Robson (1980) and Earlé and Grobler (1987). Each of the 12 leaves on the rose is used to show the presence or absence of the species in that month in that grid-cell. The resulting map is so cluttered that it is quite impossible to separate out the spatial and temporal components. Multi-factor roses are even less satisfactory, see the attempt by Kemp, Kemp & Tarboton (1985).
2) Season-by-season or month-by-month maps shown side-by-side are a much better alternative and effectively show seasonal trends; e.g. Hockey, Underhill, Neatherway & Ryan (1989: 146-147) for the European Bee-eater *Merops apiaster*.
3) Histograms for individual regions, or the region as a whole, also adequately show seasonality. If the seasonal pattern is similar across the entire region then only one histogram is necessary. Regional variations are best displayed separately as has been done most effectively for butterflies in Britain (Heath, Pollard & Thomas 1984).

Breeding:

Breeding is most often displayed as a subset of general distribution (e.g. as a filled-in circle) or is displayed separately.

Cartography is a subtle art and the views presented here are my own. Without due care being paid to the design and presentation of spatial data it is possible to inhibit the reader's understanding of the geographic distribution and status of a species.

3.2.10 Breeding records: Distribution and Seasonality

It is obvious that the best way to map the breeding distribution of a colonial species is to visit all the major colonies and enumerate them directly. The SABAP field cards (= check lists) are likely to under-report the number of breeding localities, to say nothing of their inability to provide numeric estimates of the numbers of pairs breeding. Notwithstanding this, it is important to evaluate the SABAP data-set as a potential source of breeding information.

Distribution

The breeding data from the SABAP field cards are summarized by grid-cell (Table 3.24; Figure 3.43) and are compared with the known Cape Vulture breeding colonies (Table 3.25; colony data are from section 3.1 above). Of these 42 grid-cells, for which there are 174 breeding records, at least 19 grid-cells (i.e. 45%) contain one, or more breeding colonies and these account for 142 of the breeding records (81%). Those sites marked as 'Questionable' are so far from existing, extant Cape Vulture colonies as to be unacceptable. In fact, 23 (i.e. 55%) of the SABAP grid cells reporting 'breeding' for the Cape Vulture do not contain a breeding colony at all! Thus the SABAP breeding data are of little value for the Cape Vulture. The original field cards should be scrutinized by the SABAP staff and returned to the respective Regional Atlas Coordinators with a request for further substantiating information.

Seasonality

With the exception of the southern Cape breeding records, all other January to April and December breeding records should be rejected unless the observers can provide corroborative information. The breeding records from the Kruger National Park, Kalahari Gemsbok National Park and Mkuzi Nature Reserve are certainly African Whitebacked Vultures, not Cape Vultures. Furthermore, it is important to check on the dates of each of these records; I would suspect that the Ghost Mountain record is from the historical Natal data, i.e. pre-1980. To test for seasonality two 'models' are proposed: uniformity and a simple Fourier series.

Model One: Uniform.

It is hypothesized that the proportion of Cape Vulture breeding records should be constant throughout the year. This can be tested using the Chi-squared test. Let b_i be the number of breeding records in the i^{th} month out of m_i sight records. Thus there will be $B = \Sigma b_i$ breeding records in the whole year out of $M = \Sigma m_i$ sight records and the average proportion of breeding records will $P = B/M$. Thus the number of breeding records expected in month i will be $p_i = m_i{*}P = m_i{*}B/M$. A constraint on the use of the chi-squared test is that the minimum expected number of observations in each cell should be at least two, but preferably five. In addition there must be at least two cells so that there can be at least one degree of freedom. Thus only those four ¼° by ¼° grid-cells with at least ten breeding records may be tested (flagged in Table 3.24). Only one of the four localities has a statistically significant deviation from uniformity: Balloch.

No.	Map	Chi-squared	Degrees of freedom	Probability	Locality
13	2527CD	1.6851	1	0.19424	Roberts' Farm
15	2527DC	2.2176	1	0.13644	Skeerpoort
28	3027DA	9.9809	1	0.00158	Balloch
42	3420BC	6.5509	8	0.58576	Potberg

It is suspected that the breeding records at Potberg come from fledglings as well as from nests thus masking the known breeding seasonality. To tease apart these two components the breeding data need to be broken down by breeding code (see breeding codes in section 3.2.2 above).

Table 3.24

Seasonal breeding records from the SABAP data-set.

No.	MAP	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total	
1	2229DC	-	-	-	-	-	-	2	-	-	-	-	-	2	
2	2231CD	-	-	-	-	-	-	-	-	-	-	-	1*	1	
3	2329AB	1*	-	-	-	-	-	-	-	-	-	-	-	1	
4	2329CB	1*	-	-	-	-	-	-	1	-	1	-	-	3	
5	2331AB	-	-	-	-	-	1	-	-	-	-	-	-	1	
6	2426BB	-	-	-	-	1	-	-	-	-	-	-	-	1	
7	2427BC	-	-	-	-	-	-	-	1	2	-	-	-	3	
8	2427CB	-	-	-	-	-	-	-	-	-	-	-	1*	1	
9	2427CD	-	-	-	-	-	-	-	-	-	1	-	-	1	
10	2429CC	-	-	-	-	-	-	-	-	1	-	-	-	1	
11	2430BD	-	-	-	-	1	-	-	1	1	-	-	-	3	
12	2520BC	-	-	-	-	-	-	-	-	-	1	-	-	1	
13	2527CD	-	-	-	1*	2	1	1	2	4	2	-	-	13	§
14	2527DB	-	-	-	-	1	-	-	-	-	-	-	-	1	
15	2527DC	1*	-	-	-	2	2	3	1	2	3	1	1*	16	§
16	2527DD	-	-	-	1*	-	-	-	-	2	-	-	-	3	
17	2732CA	-	-	-	-	-	-	-	-	2	-	-	-	2	
18	2732CB	-	-	-	-	-	-	-	-	-	1	-	-	1	
19	2828DB	-	-	-	-	-	-	-	-	-	-	-	1*	1	
20	2829AD	1*	-	-	-	-	-	-	-	-	-	-	-	1	
21	2829CA	-	-	-	-	-	1	1	2	-	-	-	-	4	
22	2928AB	-	-	-	-	-	-	-	-	1	-	-	-	1	
23	2928BC	-	1*	-	-	-	-	-	-	-	-	-	-	1	
24	2929BA	-	-	1*	-	-	-	-	-	-	-	-	-	1	
25	3025BC	-	-	-	1*	-	-	-	-	-	-	-	-	1	
26	3027AC	-	1*	-	-	-	-	-	-	-	-	-	-	1	
27	3027CD	-	-	-	-	-	-	-	-	1	-	-	-	1	
28	3027DA	-	-	-	-	-	1	3	1	4	3	3	-	15	§
29	3027DB	1*	-	-	-	-	-	-	-	-	-	1	1*	3	
30	3030CC	-	-	-	-	-	-	-	-	1	-	-	-	1	
31	3127BB	-	-	-	-	-	-	1	-	-	-	-	-	1	
32	3127BD	2*	-	-	-	-	2	-	-	-	-	-	-	4	
33	3127CB	-	-	-	-	-	-	-	-	1	-	-	-	1	
34	3129BB	-	-	-	-	-	-	-	1	-	-	-	-	1	
35	3129BD	1*	-	-	-	-	-	-	-	-	-	-	-	1	
36	3130AA	-	-	-	-	-	1	1	-	-	-	-	-	2	
37	3227AA	-	-	-	-	-	-	-	-	-	1	-	-	1	
38	3228BA	-	-	-	-	2	-	2	-	-	-	-	-	4	
39	3228CA	-	-	-	-	-	-	-	-	-	1	-	-	1	
40	3321DA	-	-	-	-	-	1	1	1	1	1	-	-	5	
41	3420AD	-	1	-	-	-	-	-	1	-	-	-	-	2	
42	3420BC	5	3	3	2	4	6	5	6	9	9	7	6	65	§
	Total	13	6	4	5	13	16	20	18	32	24	12	11	174	

* Breeding records outside of the period May-November, except in the southern Cape are suspect; breeding season is much later in southern Cape (A.F. Boshoff pers. comm.).

§ A sufficient number of breeding records exist to perform a chi-squared test.

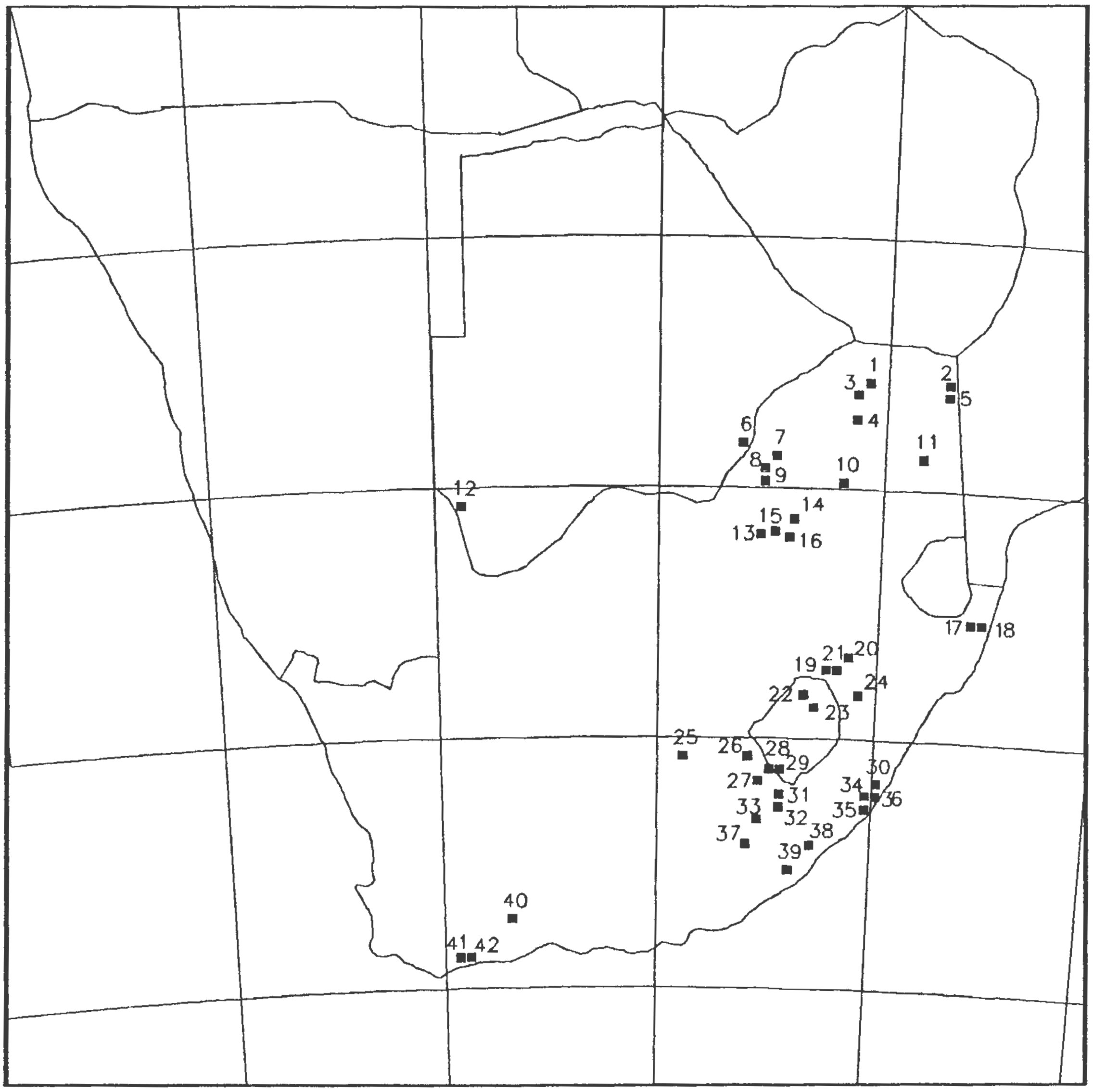


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Figure 3.43 Location of the 42 ¼° by ¼° grid-cells for which there are breeding records of Cape Vultures. Site numbers are those shown in Table 3.24.

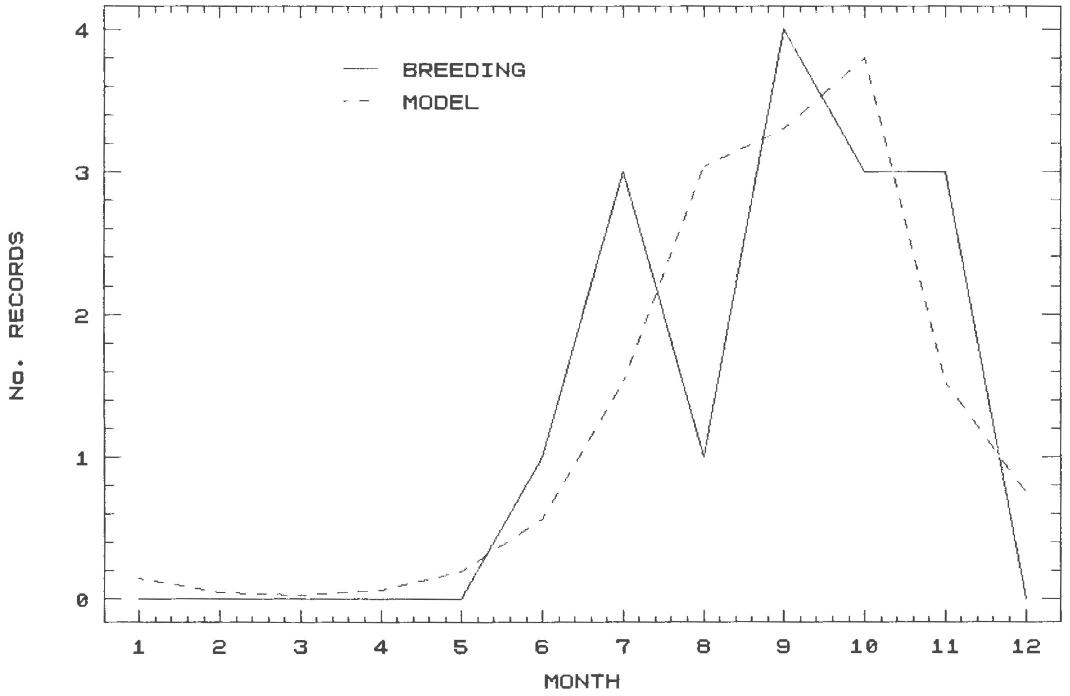

Figure 3.44 The number of breeding records submitted per month (in the SABAP data-set, line 28 of Table 3.24) for the ¼° by ¼° grid-cell 3027DA (Balloch) compared with Fourier model fitted using GLM.

Model Two: Simple Fourier series.

Using the above symbolism the binomial probability, p_i may be modelled using the Fourier series (as suggested by W. Zucchini and L.G. Underhill pers. comm.) to be fitted using a generalized linear model (McCullagh & Nelder 1989: 98 ff.). Let c_i be the linear predictor for the i^{th} month:

$$c_i = a_0 + b_0 * \mathrm{SIN}(2\pi(i+\Phi)/12) \qquad \text{[Angle measured in radians]}$$

Where b_0 is the amplitude and Φ is the phase shift. Using simple trigonometry, i.e. $\mathrm{SIN(A+B)=SIN(A)*COS(B)+SIN(B)*COS(A)}$, the above equation reduces to:

$$c_i = a_0 + a_1 * \mathrm{SIN}(\pi i/6) + a_2 * \mathrm{COS}(\pi i/6)$$

where a_1 and a_2 may be related to b_0 and Φ via:

$a_1 = b_0 * \mathrm{COS}(\Phi\pi/6)$ and $a_2 = b_0 * \mathrm{SIN}(\Phi\pi/6)$

The probability of a breeding record, p_i in the i^{th} month is fitted to the linear model c_i via the logit link function:

$$\mathrm{Log}_e((p_i/(1-p_i)) = c_i$$

The constants (i.e. a_0, a_1 and a_2) are fitted using a generalized linear model (by means of the GENSTAT 5 package, Anon. 1988). The two parameters, Φ and b_0 may be computed from:

$$\Phi = 6*[\arctan(a_2/a_1)]/\pi \text{ and } b_0 = [a_1^2+a_2^2]^{1/2}$$

Table 3.25

Evaluation of breeding records from the SABAP data-set.

(Breeding colony data come from section 3.1 above).

No.	Map	Total	Colony	Comments
1	2229DC	2		Questionable
2	2231CD	1		Questionable
3	2329AB	1		AA = Blouberg
4	2329CB	3		CD = Madikoto
5	2331AB	1		Questionable
6	2426BB	1		Questionable
7	2427BC	3	Groothoek	
8	2427CB	1		Confused with Kranzberg or Groothoek?
9	2427CD	1		Confused with Kranzberg or Groothoek?
10	2429CC	1		Questionable
11	2430BD	3		= Manoutsa?
12	2520BC	1		Questionable
13	2527CD	13	Roberts' Farm	
14	2527DB	1		Old record at Nooitsomethingorother?
15	2527DC	16	Skeerpoort	
16	2527DD	3		Questionable
17	2732CA	2	Ghost Mountain	Old record?
18	2732CB	1		Mkuzi = African Whitebacked Vulture?
19	2828DB	1	Witsieshoek	
20	2829AD	1	Rensbergskop	
21	2829CA	4	Mount Lebanon	
22	2928AB	1	Vulture's Peak	
23	2928BC	1	Thaba-Tseka	
24	2929BA	1	Ntabamhlope	
25	3025BC	1		Questionable
26	3027AC	1		Questionable
27	3027CD	1		= Karnmelkspruit?
28	3027DA	15	Balloch	
29	3027DB	3	Danger's Hoek	
30	3030CC	1		Questionable
31	3127BB	1		Questionable
32	3127BD	4	Vanzylsberg	
33	3127CB	1	Indwe Poort	
34	3129BB	1		Questionable
35	3129BD	1	Mtzikaba	
36	3130AA	2	Umtamvuna	
37	3227AA	1		Questionable
38	3228BA	4	Colleywobbles	Is this all?
39	3228CA	1		Questionable
40	3321DA	5	Badspoort	
41	3420AD	2		Questionable
42	3420BC	65	Potberg	
	Total	174		

Where:

Map = The ¼° by ¼° grid-cell.

Total = No. of field cards for that ¼° by ¼° grid-cell with Cape Vulture breeding records, over all months, over all years.

Colony = Name of major colony nearest to the ¼° by ¼° grid-cell.

Table 3.26

Comparison of observed and fitted number of breeding records per month at Balloch.

Month	X	Y	Field cards	Breeding records	Fitted value
1	0.87	0.5	3	0	0.145
2	0.5	0.87	3	0	0.049
3	0.0	1.	3	0	0.033
4	-0.5	0.87	4	0	0.066
5	-0.87	0.5	4	0	0.194
6	-1.	0.	3	1	0.561
7	-0.87	-0.5	3	3	1.530
8	-0.5	-0.87	4	1	3.042
9	0.0	-1.	4	4	3.298
10	0.5	-0.87	5	3	3.803
11	0.87	-0.5	3	3	1.530
12	1.0	0.0	4	0	0.749

The reverse transformation is:

$$p_i = \exp(c_i)/(1+\exp(c_i))$$

This model is fitted to that grid-cell (i.e No.28, Table 3.24) which showed a significant chi-squared value.

Putting $X = \mathrm{SIN}(\pi i/6)$ and $Y = \mathrm{COS}(\pi i/6)$ and fitting the model yields the following results:

Variable	Estimate	s.e.	t
Constant	-1.469	0.604	-2.43
Y	-3.017	0.895	-3.37

X- not fitted because the t-value was not statistically significant at 5%

Solving for the constants gives Φ = 9 months, a_0 = -1.469 and b_0 = -3.017. Using these constant the fitted values may be tabulated and compared with the observations (Figure 3.44; Table 3.26).

It can be seen that the fit is good and the model predicts a maximum number of breeding records in October. It is likely, with more data, that this method can be employed to good effect in modelling breeding seasonality.

3.2.11 Comparison of Cape Vulture maps

A number of maps have been constructed of the Cape Vulture's geographical distribution and these can be categorized into four broad classes, dependent on their data source.

1) Individual records displayed using one or more symbols (e.g. Brooke 1984: 67, see Figure 3.45 A; SABAP data, see section 3.2.5 above and Figure 3.45 B).
2) Binary presence and absence maps showing some generalized distribution (e.g. Maclean 1985, see Figure 3.45 C).
3) Maps generated from an enumeration of roosts and breeding colonies (i.e. from the Site Register, see section 3.1 above and Figure 3.45 D).
4) Reporting rates based on the proportion of bird field cards with Cape Vultures sighted (i.e. the SABAP data-set, see section 3.2.5 above).

Each of these maps will now be discussed and comparisons will be made among them.

Maps of individual records

The best published map of the distribution of the Cape Vulture based on individual records is that produced by Brooke (1984: 67) in which the records from 1800 to 1969 are shown as open circles while those from 1970 to about 1983 are depicted as closed circles (Figure 3.45 A). This two-symbol map gives some idea of the range contraction of the species, especially in the Transvaal and Karoo (i.e. these are the localities with the most open circles). This map may be compared with the data-set from SABAP (Figure 3.45 B) which is based on field card data collected during the period 1980 to early 1991 (J.A. Harrison pers. comm.). From the juxtaposition of these two figures it is possible to see that the modern (SABAP) map shows more sightings in the eastern Transvaal Lowveld and Kruger National Park, central Karoo and western and northwestern Transvaal while the older map shows more sites in the southern and southeastern Transvaal, northern Natal and Orange Free State.

Binary "Species' Distribution maps"

The generalized map in Maclean (1985) is typical of Cape Vulture distribution maps found in handbooks and field guides (Figure 3.45 C). When compared with the known sightings maps (i.e. Figures 3.45 A & B) and the map of all putative sites (Figure 3.45 D) it is seen that the species' range as depicted by Maclean's map is generally greater than the convex polygon enclosing all known sightings as well as almost all the putative sites. In other words, it is too optimistic. It includes all known records, and the spaces in between. It makes no allowance for range contraction.

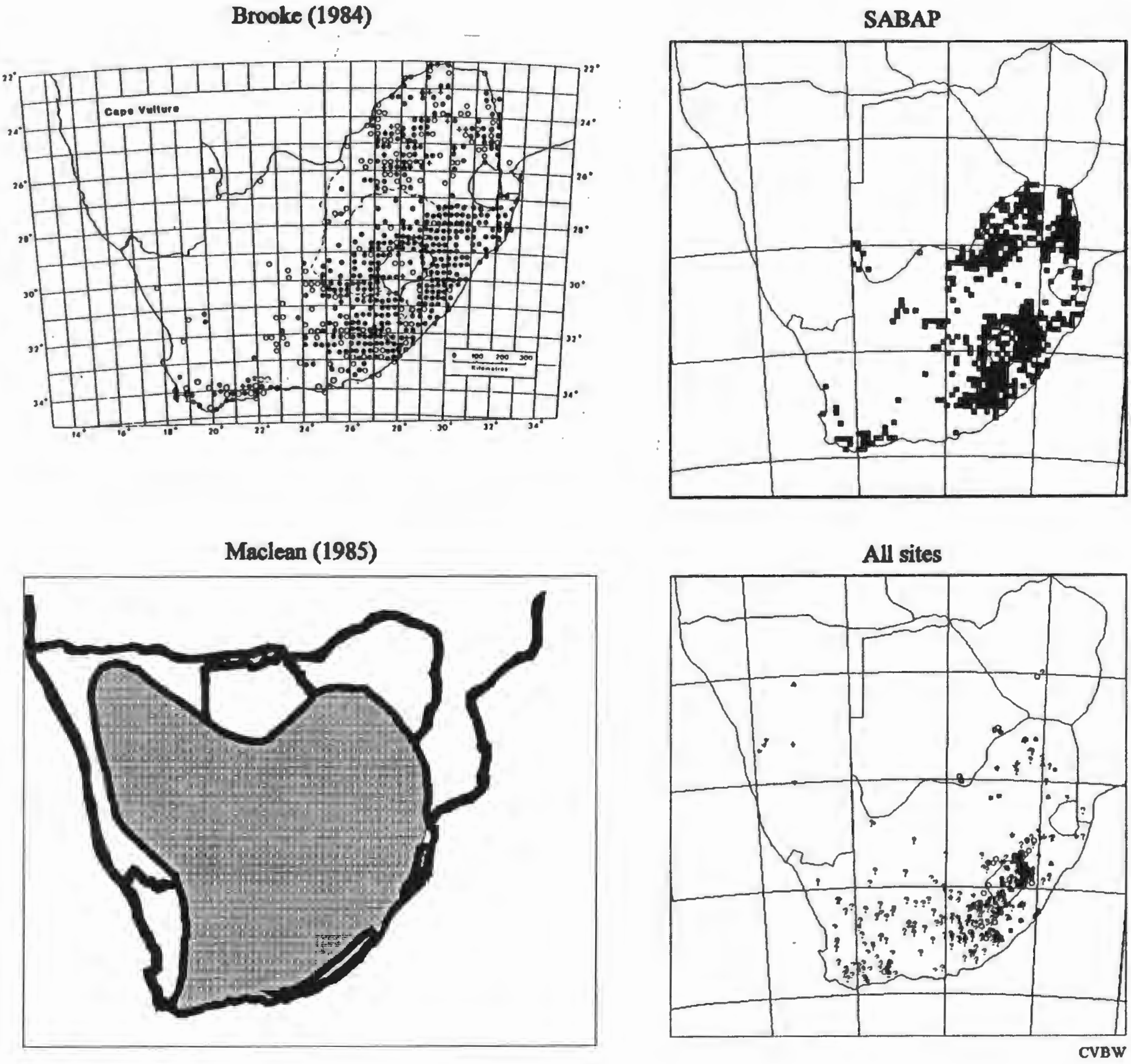

Figure 3.45 Comparison of presence and absence maps of the Cape Vulture's distribution. A. Brooke (1984: 67) - open circles represent records from 1800 to 1969 and closed circles from 1970 to about 1983. B. SABAP data-set from about 1980 to May 1991 (excluding data from Namibia, Botswana and Zimbabwe). C. Roberts' Birds of southern Africa (Maclean 1985) - an example from a field guide. D. All putative Cape Vulture sites.

Reporting rate map

From the binomial kriging of the reporting rate (see section 3.2.5 above) it is possible to generate a contour map of sighting probabilities, i.e. the likelihood that a typical observer will see a Cape Vulture while assembling a field card in a given grid-cell. It is argued above (section 3.2.5) that the 3% contour gives a binary 'distribution map' which is broad enough to show all the places where seeing a Cape Vulture is reasonable while not being so general as to include vagrants (see Figure 3.40). The SABAP team (J.A. Harrison pers. comm.) recommend a cut-off of 1.5 to 2% but it was found, for the Cape Vulture, that this included too many vagrants and errors. This map (i.e. Figure 3.40) clearly shows that the Cape Vulture has two major 'heart-lands'. The one in the Transvaal and Botswana and the other in Lesotho, Natal Drakensberg, Transkei and Eastern Cape. The are also smaller 'islands' in the Karoo, northern Cape and southwestern Cape.

Reporting rate map and active sites

An independent measure of the distribution of the Cape Vulture comes from the counts of birds at roosts and breeding colonies. It is possible to compare these counts with the SABAP-derived distribution map by overlaying the active sites atop the 3% reporting rate distribution (Figure 3.46). It is immediately apparent that the active sites are contained entirely within the SABAP data, except for those sites in Namibia and Zimbabwe for which there were no SABAP data. This shows that all known Cape Vultures sites are contained within those regions in which Cape Vultures are seen by bird watchers, and reported to SABAP.

Reporting rate map and uniform disc model: overlaying the distributions

Thus far no numerical measures of agreement have been made of the degree to which the two spatial data-sets (i.e. SABAP and Site Register) agree in their geographical distributions. The first way of measuring the overlap is to count directly the match between these two distributions. This is done in the following fashion. Each of the active Cape Vulture sites (i.e. roost or breeding colony) is surrounded by a disc of radius R km and the Cape Vultures are assumed to be spread out equally over the disc (see section 3.2.1 above for computational details). Each of the ¼° by ¼° grid-cells is taken one at a time and is classified into one of four classes in the following fashion.

Positive match: Uniform disc model predicts density>0 AND SABAP reporting rate>0
Commission: Uniform disc model predicts density>0 BUT SABAP reporting rate$=0$
Omission: Uniform disc model predicts density$=0$ BUT SABAP reporting rate>0
Negative match: Uniform disc model predicts density$=0$ AND SABAP reporting rate$=0$

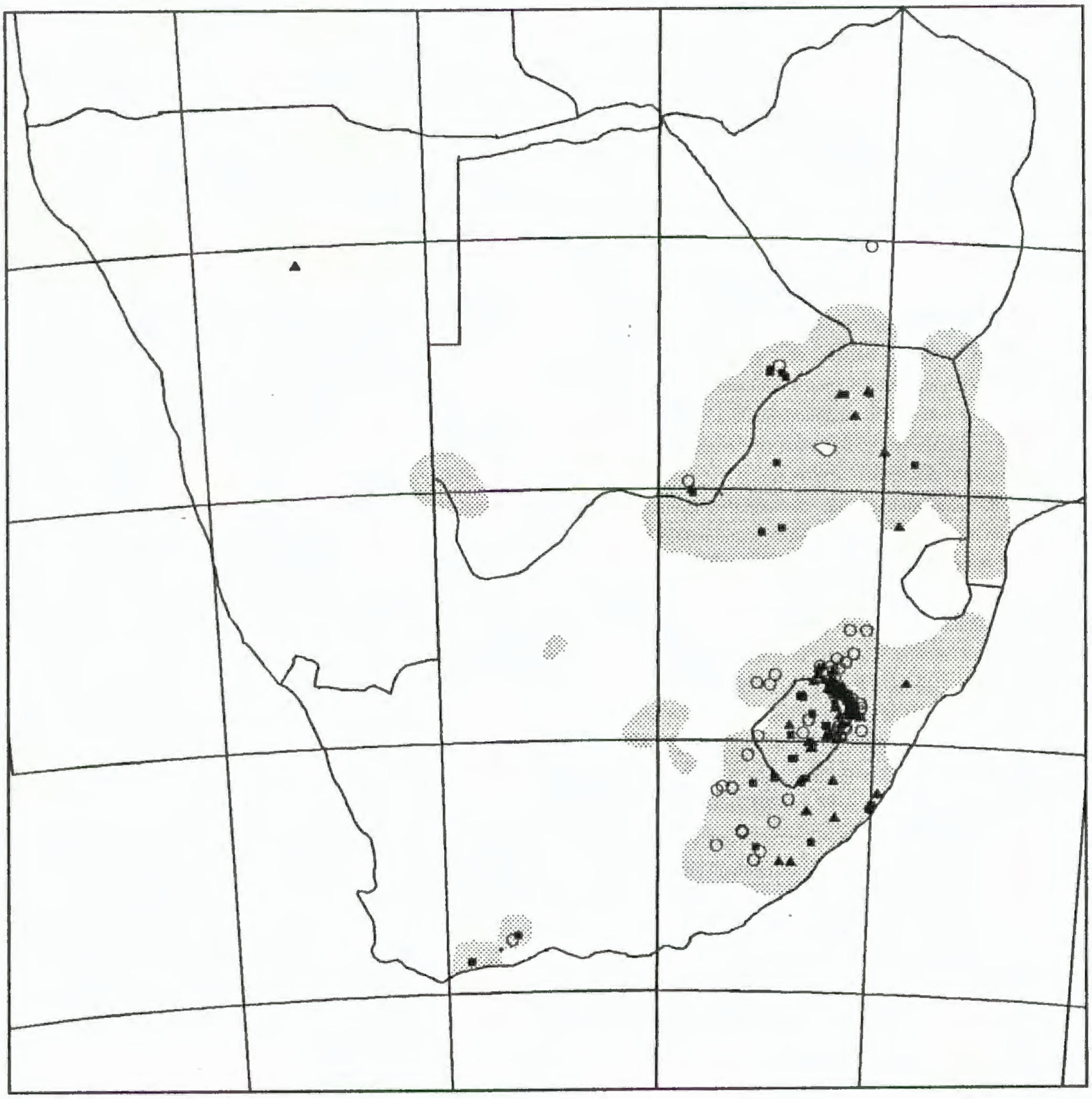

Figure 3.46 Comparison of the location of all active Cape Vulture sites (i.e. roosts, satellites and nucleus colonies shown as circles, triangles and squares respectively) with the distribution map based on the kriged reporting rate of 3% (shaded region: SABAP data). Note that there are no SABAP data from Namibia, Botswana and Zimbabwe.

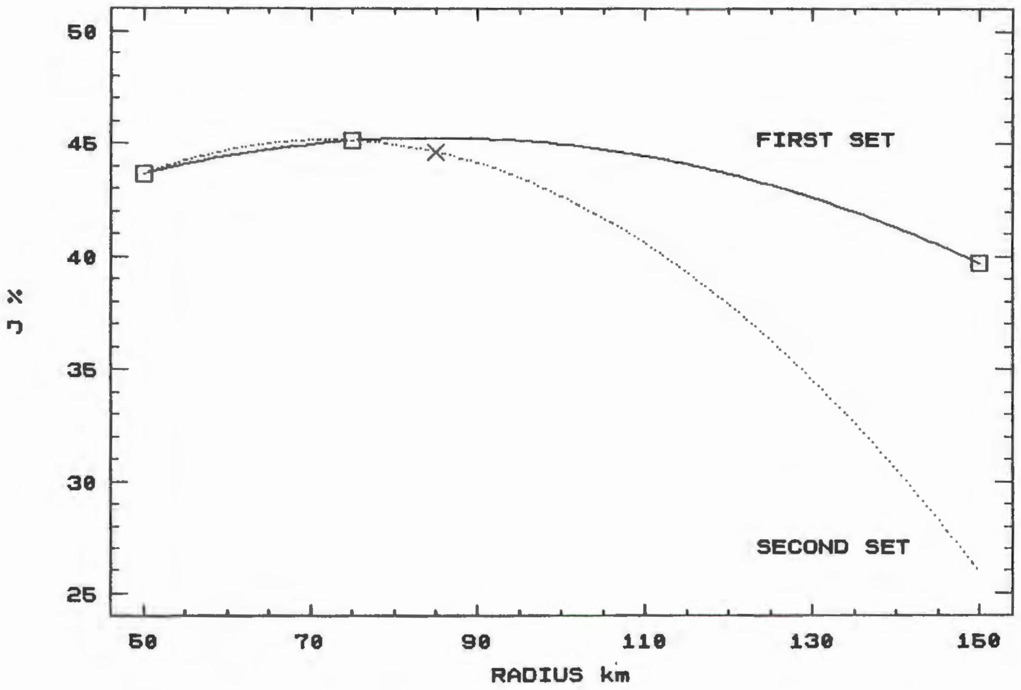

Figure 3.47 Agreement between the SABAP sightings data and the roost and colony data. Overlap is measured by the Jaccard coefficient, J. The quadratic fitted to the 'first set' is based on evaluations of J at R = 50, 75 and 150 km. An optimum is predicted at R = 85.07 km. The quadratic fitted to the 'second set' is based on evaluations at R = 50, 75 and 85.07 km.

The uniform disc model was computed for radii of 50, 75 and 150 km and the geographical variations in Cape Vulture densities plotted (Figure 3.25). For each case the numbers of positive and negative matches, commissions and omissions were counted (Table 3.27) and the Jaccard coefficient, J was computed as a measure of agreement, or overlap.

J = Positive matches/(Positive matches + commissions + omissions)

This coefficient varies from 0% (= no overlap) to 100% (perfect overlap) while taking both omissions and commissions into account (Sokal & Sneath 1963: 128 ff.). Negative matches are not included because knowing that two distributions both do not occur in a given area contributes no additional information (loc. cit.).

It can be seen that J rises as R increases from 50 to 75 km but decreases when R reaches 150 km. This is because increasing R initially increases the disc size, so reducing the number of omissions but later the disc becomes so big that the number of commissions grows disproportionately.

Table 3.27

Agreement between SABAP data and uniform disc model as measured by the Jaccard coefficient, J. (J was evaluated for R = 50, 75 & 150 km and an optimum was predicted at R = 85.07 which was then evaluated.)

Radius km	50	75	150	85.07
Negative matches	1235	1127	808	1075
Positive matches	312	371	453	390
Commissions	203	310	629	362
Omissions	200	141	59	122
Jaccard coefficient	43.64%	45.13%	39.70%	44.62%

Plotting J vs R (Figure 3.47) and fitting a quadratic for radii R = 50, 75 and 150 km (i.e. the 'first set') yields:

$J = 35.71 + 0.2246*R - 0.00132*R^2$

This quadratic is a maximum at R = 85.07 km. Repeating the uniform disc model at R = 85.07 km yielded J = 44.6%, slightly worse than at R = 75. Fitting the quadratic a second time, but now to the data points R = 50, 75 and 85.07 km (i.e. the 'second set') yields:

$J = 28.81 + 0.4546*R - 0.00316*R^2$

Now the maximum value of J is predicted to be 45.16% at R = 71.93 km. But the incremental improvement in J is so small (about 0.03%) that the extra computation is not justified.

The overlap of these two distributions may be view pictorially (Figure 3.48) and the following conclusions draw.

1) The areas of greatest overlap are in the two 'heart-lands' of the a) Transvaal and b) Lesotho, Natal Transkei and eastern Cape.
2) The major areas of omission (i.e. SABAP data only) are in the eastern Transvaal, especially the Kruger National Park, northern Natal, the Karoo, Kalahari Gemsbok National Park and along the southern portion of the western Cape coast.
3) The areas of commission (i.e. uniform disc data) are around the major concentrations in Natal, Orange Free State, Eastern Cape, Transvaal and especially the southwestern Cape.

It is clear from this analysis that the uniform disc model is 'pushing out' too far from those areas of lower density - this is seen especially well around the southwestern Cape sites.

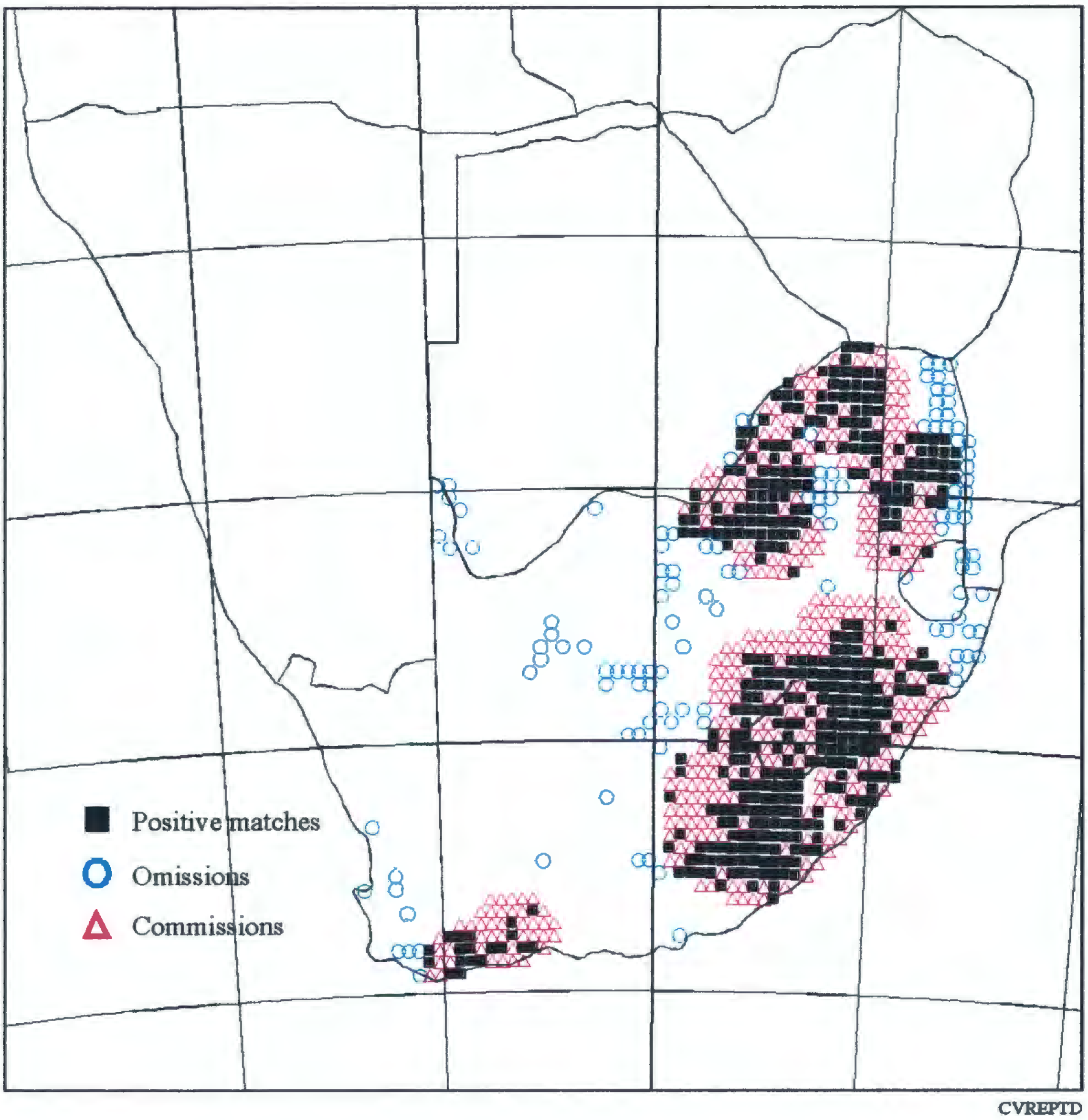

Figure 3.48 Spatial agreement between the SABAP field card data and the Site Register count data as modelled using the uniform disc model with R = 85.07 km. The omissions occur where there are SABAP sightings, but zero density and the commissions where the density is positive but there no SABAP sightings.

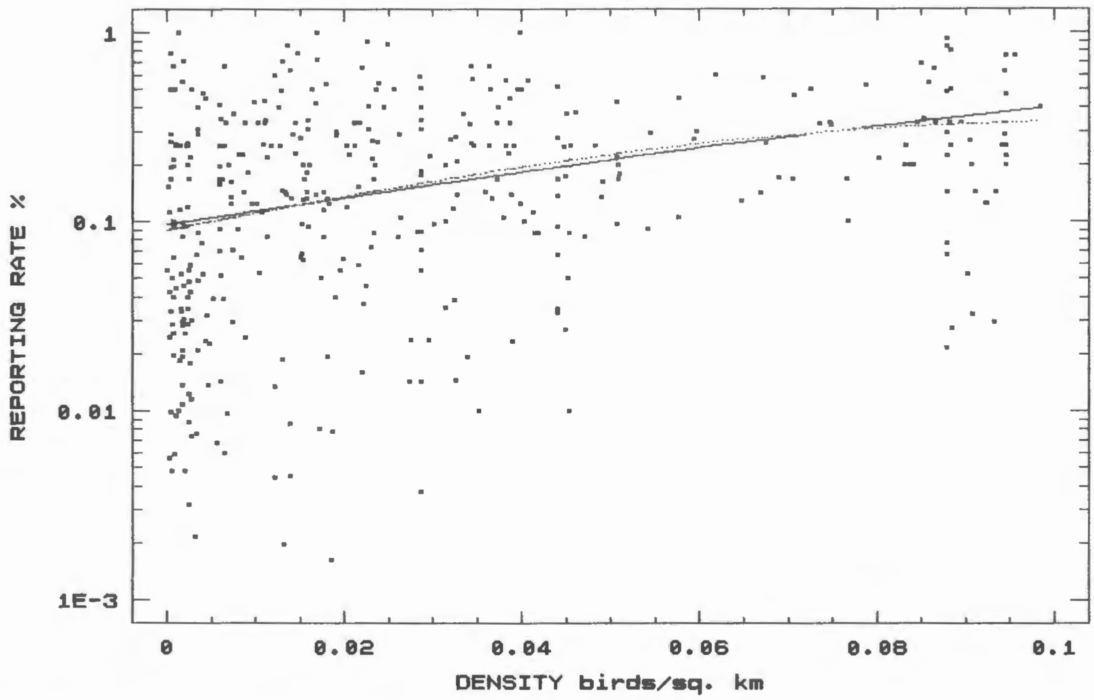

Figure 3.49 Relationship between the reporting rate (for SABAP grid cells with $r > 0$) and Cape Vulture density ($\tau > 0$, from the uniform disc model $R = 85.07$ km).

Reporting rate map and uniform disc model: modelling the reporting rate

The previous analysis measured the way in which the two distributions overlapped but gave no consideration to the degree to which the densities of the two distributions matched. To quantify the relationship between the two distributions it must be remembered that Cape Vulture density, in a given grid-cell, is measured as birds/km^2 while the reporting rate is a binomial variable with m field cards out of M reporting Cape Vultures. To model this a generalized linear model (GLM) is best used (see motivation earlier in this chapter) in which the reporting rate, r ($= m/M$) is transformed via the logit link function and then regressed against some function of density (Figure 3.49).

$\text{Logit}(r) = \text{Ln}(r/\{1-r\}) = f(\tau)$

where τ is the density measured as vultures/km^2.

A number of models were fitted and the following two were chosen.

$\text{Logit}(r) = \text{Ln}(r/\{1-r\}) = -2.2400 + 18.474*\tau$ Model D

$\text{Logit}(r) = \text{Ln}(r/\{1-r\}) = -2.3147 + 23.36*\tau - 693*\tau^3$ Model D, D3

The coefficients in the above models were all highly significant ($p < 0.001$). The curves differ by very little over the whole range of densities (Figure 3.49). While these two models do indeed follow the general trend of the data there are a number of points which do not fit the model (i.e. they have large standardized residuals).

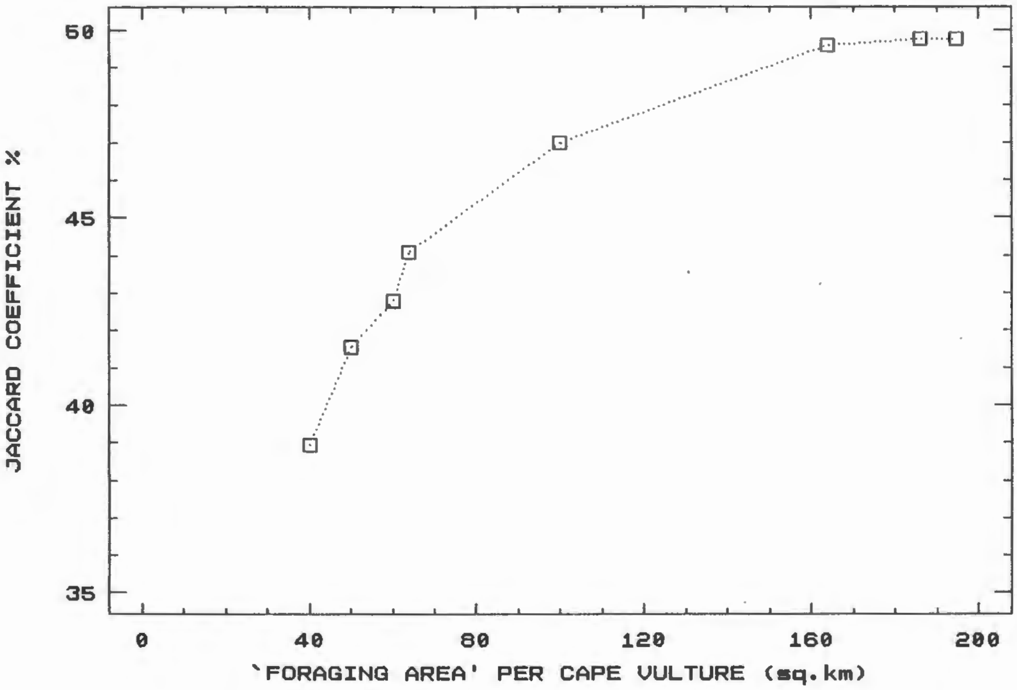

Figure 3.50 Variable disc model. Agreement between the SABAP sightings data and the roost and colony data. Overlap is measured by the Jaccard coefficient, J.

From the above analysis it seems as though the discs around the smaller sites (e.g. southwestern Cape, Natal and Lesotho) are 'pushing out' too far, when compared with the SABAP sightings data. A possible reason for this may be that birds from the bigger colonies may indeed have to go further out. These big colonies are located in cattle-ranching country, in the main, and it is likely that the food parcels are large, but sparsely distributed in space and time, thus forcing them to forage over much larger distances than birds feeding from sheep and goats.

An alternative model to the uniform disc of radius R is to assume a disc of an area proportional to the number of birds. Such a model was constructed assuming 40, 50 and then 60 km^2/bird. It was found that the match was poor when measured by the Jaccard coefficient (Figure 3.50). Increasing the area to nearly 200 km^2/bird increased the fit to nearly 50%. The best fit (J=49.7%; Figure 3.50) between the site count data and the SABAP reporting rate was for an area of 185.9 km^2/bird (Figure 3.51). Using this estimate a density map was created for all Cape Vultures (Figure 3.52 A) as well as for the number of breeding birds (Figure 3.52 B).

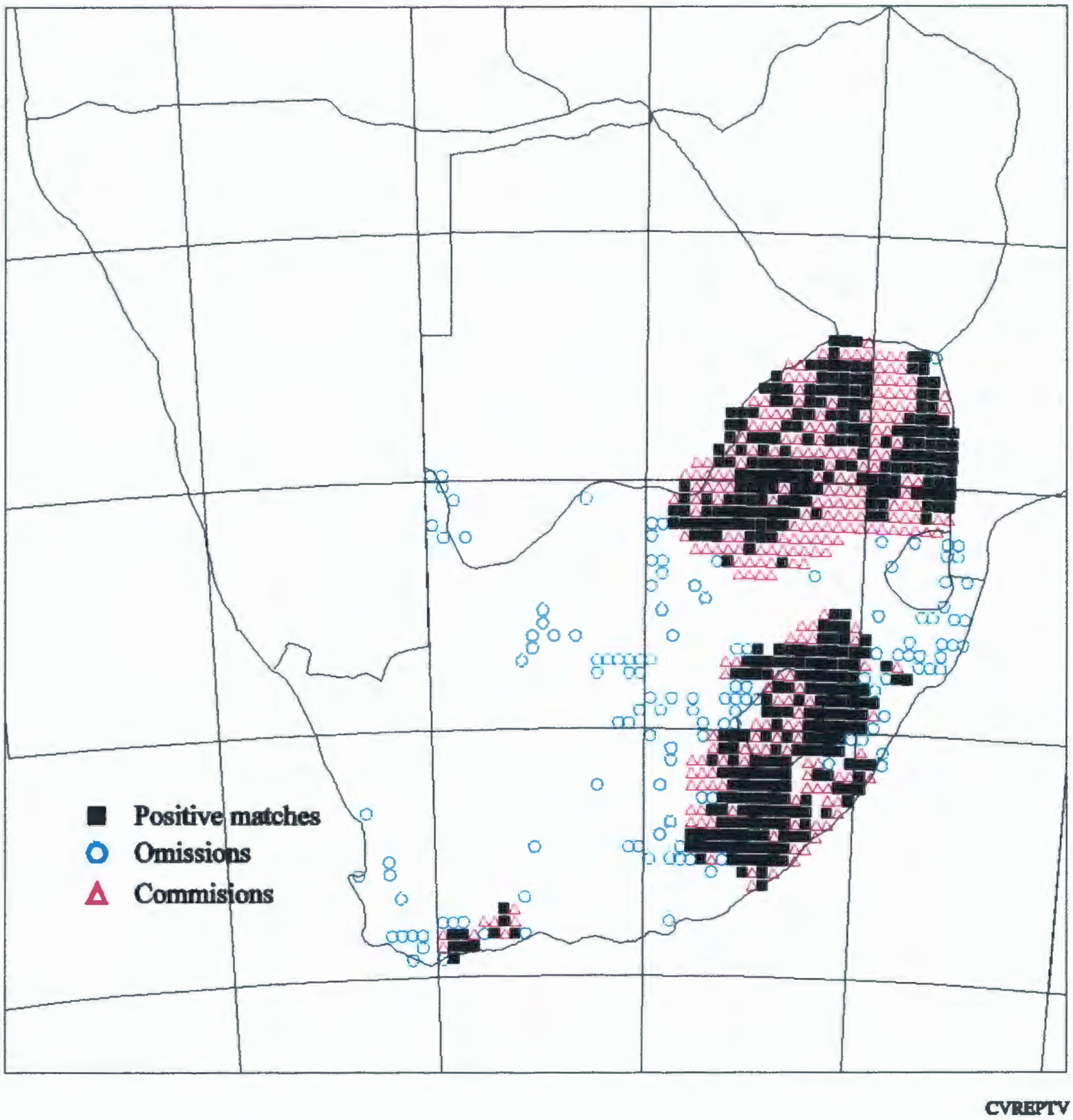

Figure 3.51 Spatial agreement between the SABAP field card data and the Site Register count data as modelled using the variable disc model with 185.9 km^2/bird. The omissions occur where there are SABAP sightings, but zero density and the commissions where the density is positive but there no SABAP sightings.

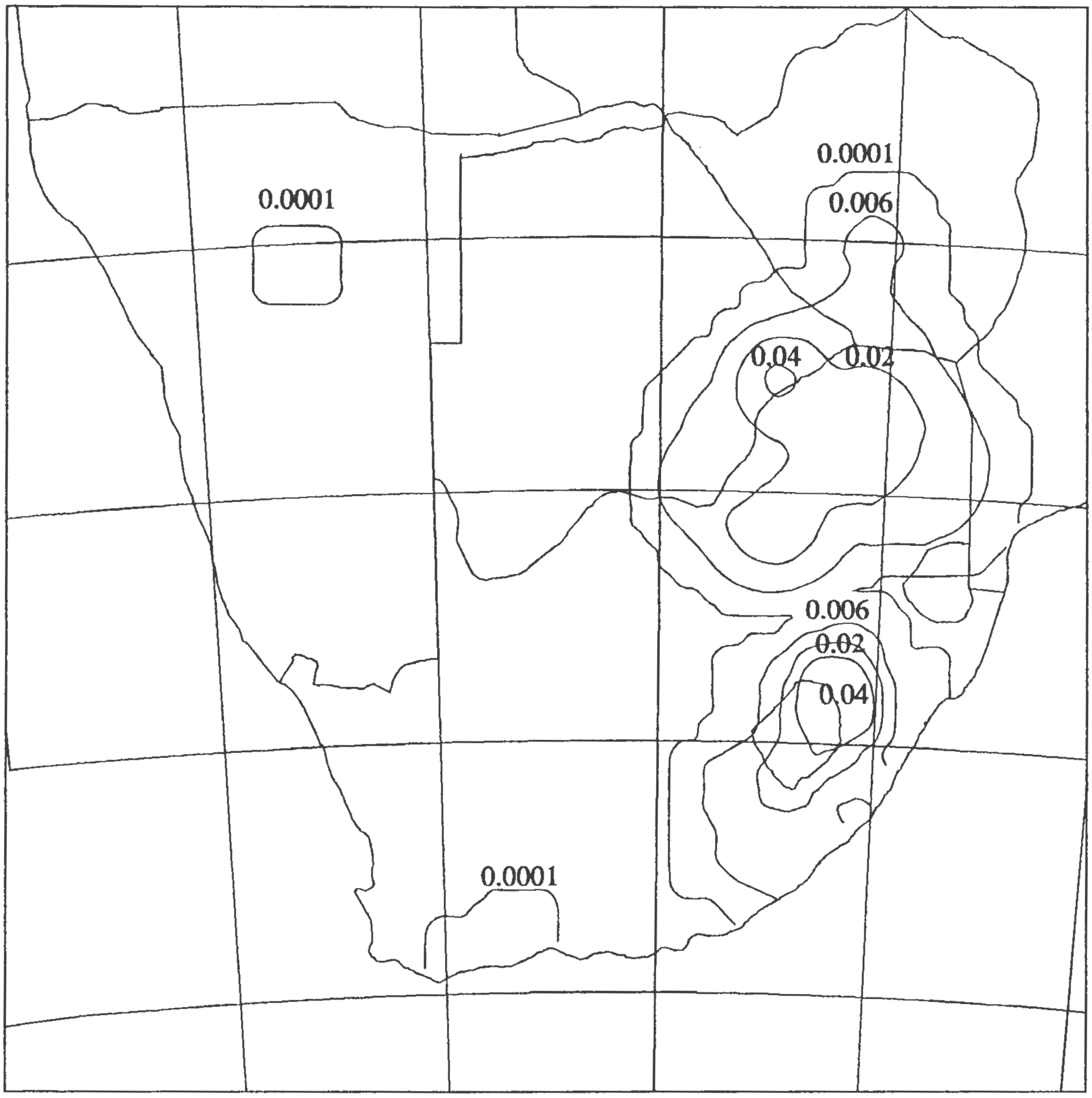

Figure 3.52 A. Cape Vulture density map based on the variable disc model assuming 185.9 km^2/bird. Density measured in birds/km^2.

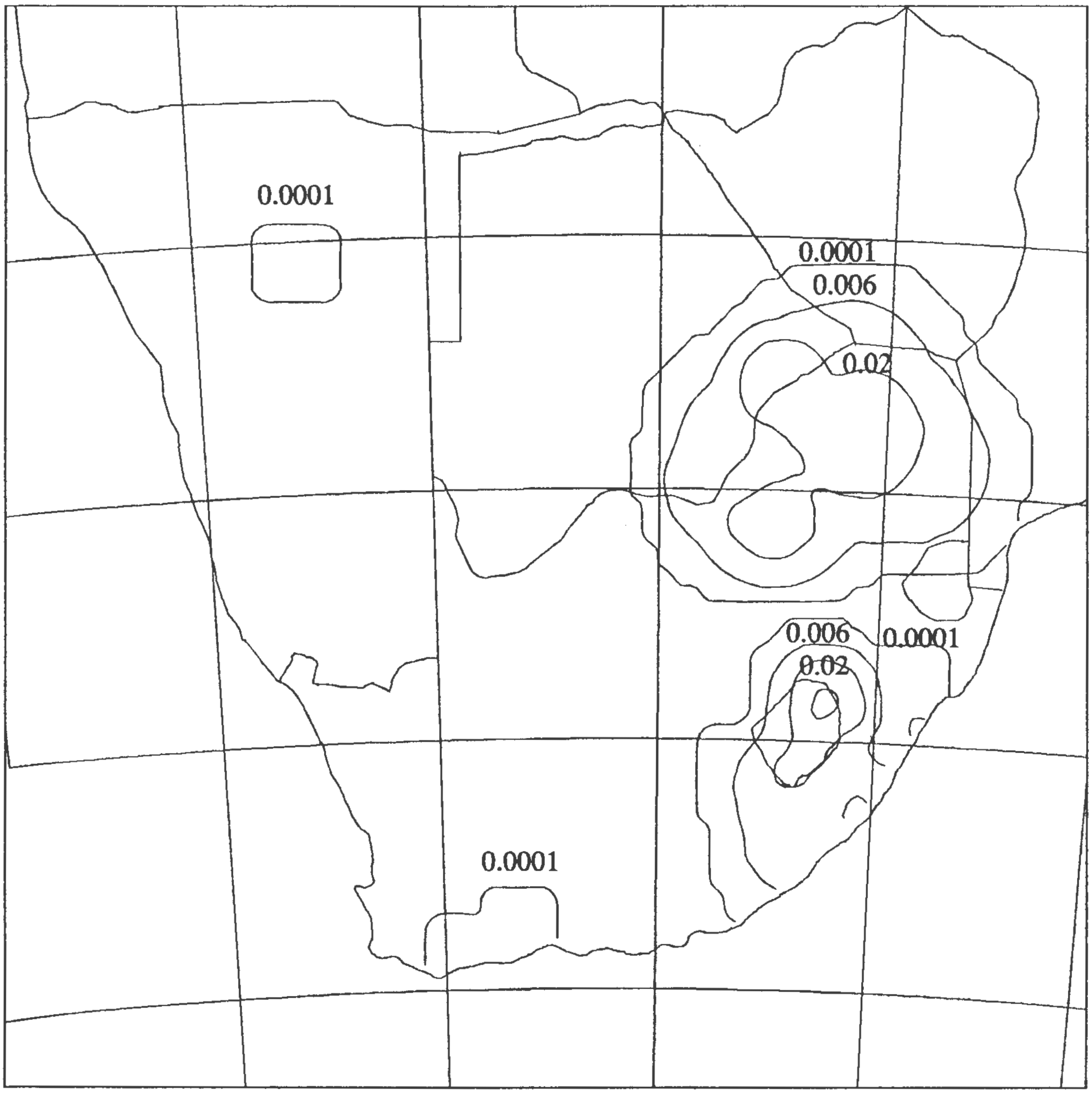

Figure 3.52 B. Density of breeding Cape Vultures based on the variable disc model assuming 185.9 km^2/bird. Density measured in birds/km^2.

3.3 Trends in numbers at sites

So far in this chapter consideration has been given to methods of assessing the extent, age- and breeding-composition and spatial distribution of the Cape Vulture but little mention has been made of the way the population is changing in time. The following questions need to be addressed:

1) From where have Cape Vultures disappeared?
2) Where have Cape Vultures appeared or reappeared? Specifically, it is important to look at colony switching.
3) At which sites are Cape Vultures currently increasing or decreasing?
4) At what rate are the numbers of Cape Vultures changing?
5) What is the spatial location of those sites which are changing? Are they at the periphery or within the core of the population?
6) Can any specific effects (e.g. disturbance, overgrazing, bush encroachment, lack of water etc.) be implicated and quantified?

It is a lot easier to pose questions than to answer them; not all of the above questions can be answered for all sites or all regions. This is a consequence of an incomplete data-set. There are enough temporal data for 14 sites from four regions to make some assessment of the way attendance at the site is changing:

Region	Site	Changing?
Botswana	Manong Yeng	Birds, increasing
	Mannyelanong	Nests, decreasing
	Manyana	Birds, abandoned
	Kukubuye	Birds, abandoned
Cape	Aasvogelvlei	Birds, abandoned
	Balloch	Stable?
	Karnmelkspruit	Birds, abandoned
	Potberg	Birds, slow decline
Namibia	Waterberg	Birds, massive decline, now increasing
Transvaal	Blouberg	Stable or increasing
	Groothoek	Stable or increasing
	Manoutsa	Stable or increasing
	Roberts' Farm	Birds, decreasing
	Skeerpoort	Birds, decreasing - now stable?

The analyses presented in this section are based on data collected up to the end of 1989 (see Forward). However, a number of important papers have been published since then and while there has not been time to incorporate their data herein, cognizance has been taken of the conclusions drawn and where it is clear that my data are inadequate or my conclusions are incorrect an appropriate modifying statement has been made.

Trends at sites in Botswana

The Cape Vulture sites in Botswana have been particularly well monitored by W.D. & R. Borello who have collated all the known records for the sites there. Four sites are analyzed.

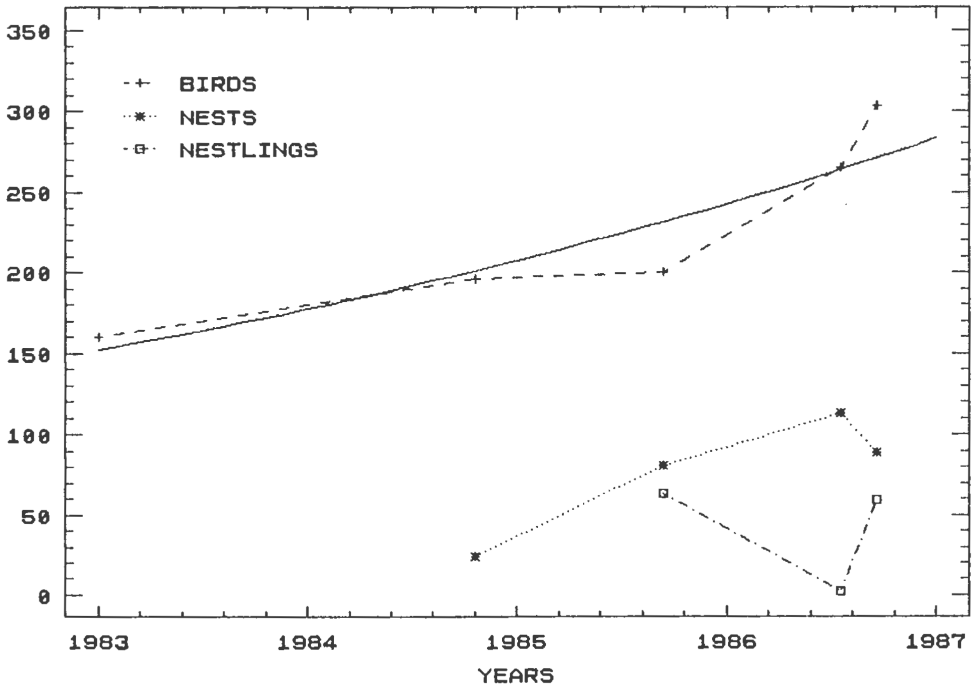

Figure 3.53 Manong Yeng (Site 21). Variation in the numbers of birds, nests and nestlings during the period 1983 to 1987, both years inclusive.

Manong Yeng, Site 21.

This recently discovered site in the Tswapong Hills was visited five times during the four year period 1983 to 1986, both years inclusive (Figure 3.53). The number of free-flying birds counted showed an increase of about 15.6% p.a. and the number of active nests also grew. The number of free-flying birds continued to increase until November 1988 when it reached a maximum of 313 (Borello & Borello 1982). Thereafter, the number of birds attending the colony decreased rapidly to a minimum of 76 in August 1990. The number of nests oscillated between 65 and 115 during the 1988 to 1990 breeding seasons, both years inclusive. The decrease in attendance at this site is ascribed to the large number of goats and cattle, and their attendant keepers, coming into the valleys below the breeding cliffs seeking browse, fodder and water. The impact of these activities has increased since 1988. In addition, a number of new schools have been established in the region during this period and the Tswapong Hills attract the new teachers who use the region for their recreational activities and so add to the disturbance.

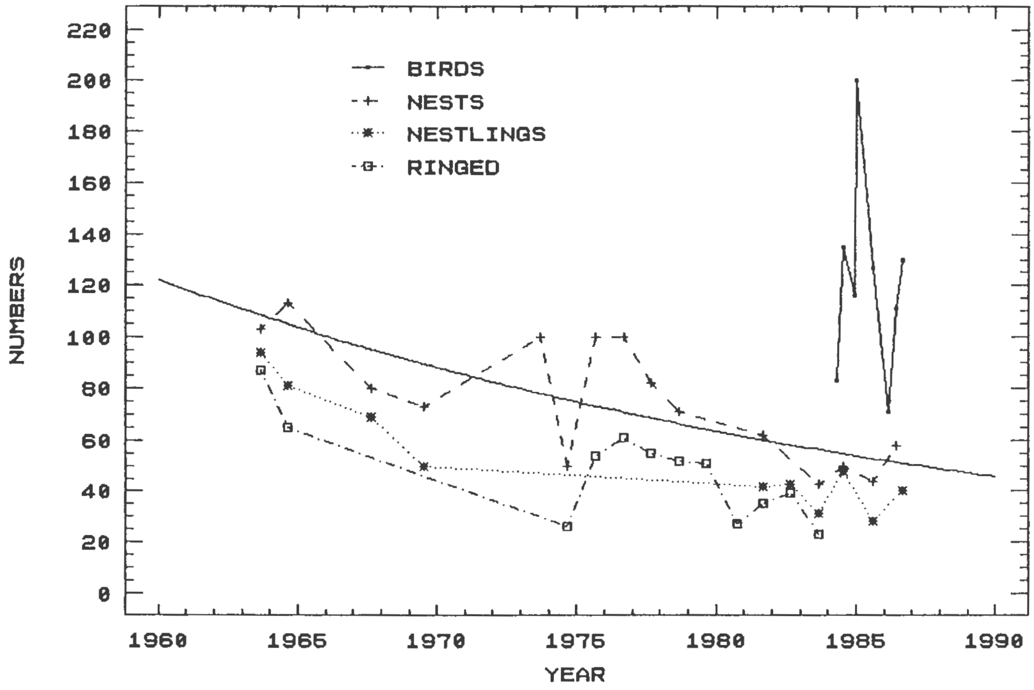

Figure 3.54 Mannyelanong (Site 44). Variation in the numbers of birds, nests, nestlings and numbers of large nestlings ringed in the period 1963 to 1986, both years inclusive.

Mannyelanong, Site 44.

The number of large nestlings ringed at Mannyelanong follows a pattern similar to the numbers of nests and nestlings counted over the period 1963 to 1985, both years inclusive (Figure 3.54). The number of nests is declining at a rate of 3.3% p.a. Unfortunately, the total number of birds at the colony were only counted for a few years in the mid-1980s. The number of free-flying birds counted at this colony has remained fairly constant during the period 1987 to 1990, both years inclusive. The range is 110 to 142 birds, mostly adult, with about 2 to 6% immatures at any one count. There has been a slow and inexorable decline in the number of active nests to less than 40 in 1990. The colony was fenced in 1984, vigilante patrols started and an education campaign initiated. However, there are still many incursions into the area by both tourists and herdsmen with their cattle and goats. Visitors climb to the top of the cliffs and have caused the birds to desert the uppermost nests. There are plans afoot to increase the protection of the area (Borello & Borello 1992).

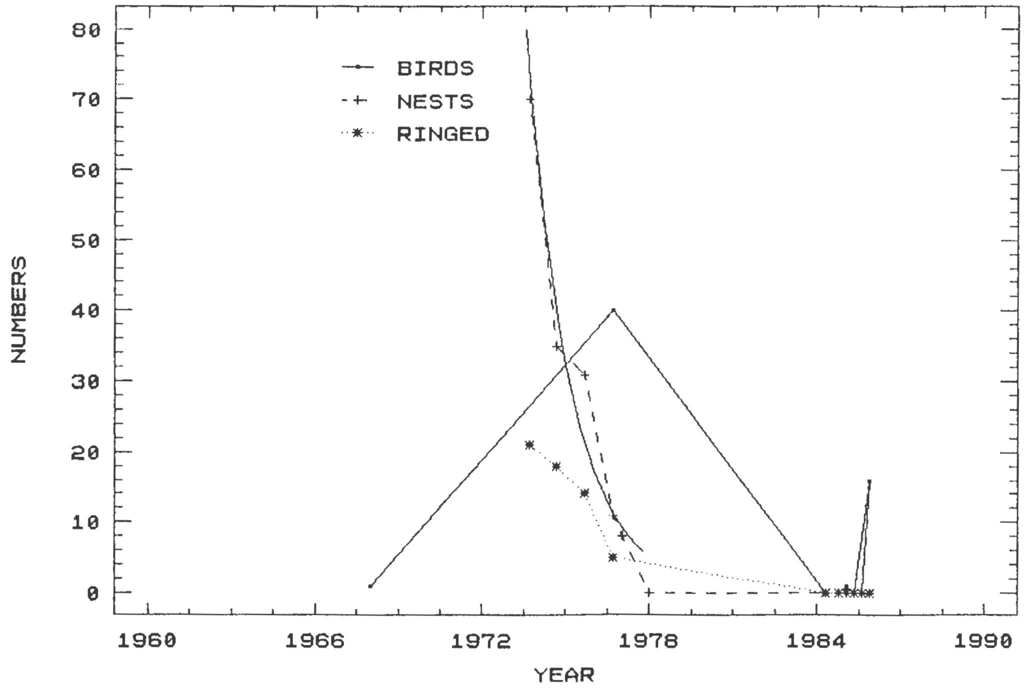

Figure 3.55 Manyana (Site 46). Variation in the number of birds and nests and numbers of large nestlings ringed in the period 1973 to 1984, both years inclusive.

Manyana, Site 46.

This site was founded in 1968 (Mundy 1983: 59-61) by birds displaced from Mannyelanong. There were 70 nests in 1973 but there colony declined to extinction by the late 1970s (Figure 3.55). The site was used sporadically thereafter as a roost. It is possible that this is an example of 'colony-switching' and needs to be investigated more carefully. Alternatively, it may be a case of displacement followed by gradual dispersal. The number of nests at the colony declined at a rate of 46.3% p.a. (Figure 3.55). The four sites in the southeast of Botswana form a close complex (i.e. Baratani Hill, Mannyelanong, Manyana and Otse Hill) and should be looked at together and while there may have been some switching between Mannyelanong and Manyana, it is likely that all the sites have declined since the mid-1970s. The reasons are not clear, but disturbance, the use of poisons and the size of local human population have all increased dramatically in the vicinity of these sites over the last few years. This site has not been visited recently but is considered still to be abandoned and likely to stay that way as a result of bush clearing and the eventual construction of a dam nearby (Borello & Borello 1992).

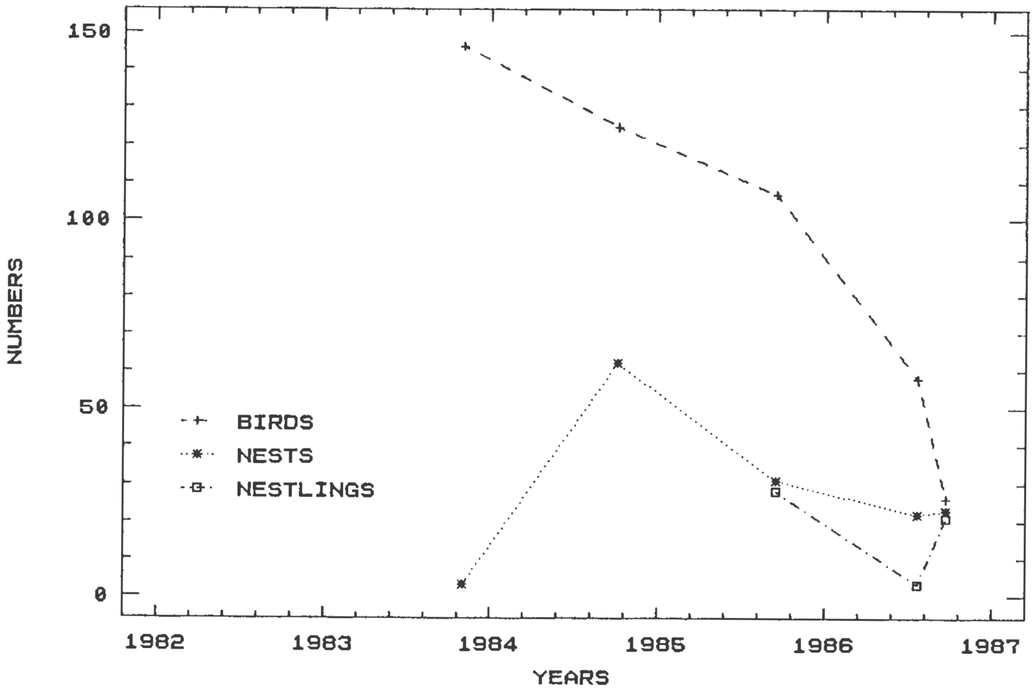

Figure 3.56 Kukubuye (Site 85). Variation in the number of birds, nests and nestlings during the period 1983 to 1987, both years inclusive.

Kukubye, Site 85.

This site showed a strong decrease in the period 1983 to 1987 (Figure 3.56) during which time the number of birds at the site declined almost to zero. This site is one of a complex of five sites in the Tswapong Hills (i.e. including Manong Yeng, Machibaba, Sebale, Bonwalenong), and is the most vulnerable in the Tswapong Hills. As Kukubuye has declined so Manong Yeng has increased. This may just be colony swapping caused by the bush clearing below Kukubye during 1985 and 1986 (Borello & Borello 1987). In July 1987 a total of 57 free-flying birds were counted but since then numbers have declined strongly and by August 1990 there were no birds to be seen at this site. Breeding also declined dramatically during this period, the last nestlings were recorded in 1988 (Borello & Borello 1992). It was also noted at the time of the 1990 census that the 'whitewash' on the cliff face had faded and it may be concluded that this site has been abandoned. Much of the once impenetrable *mopane* woodland along the base of the cliff has been cleared thus giving freer access to the colony at which there is a record of persecution (loc. cit.).

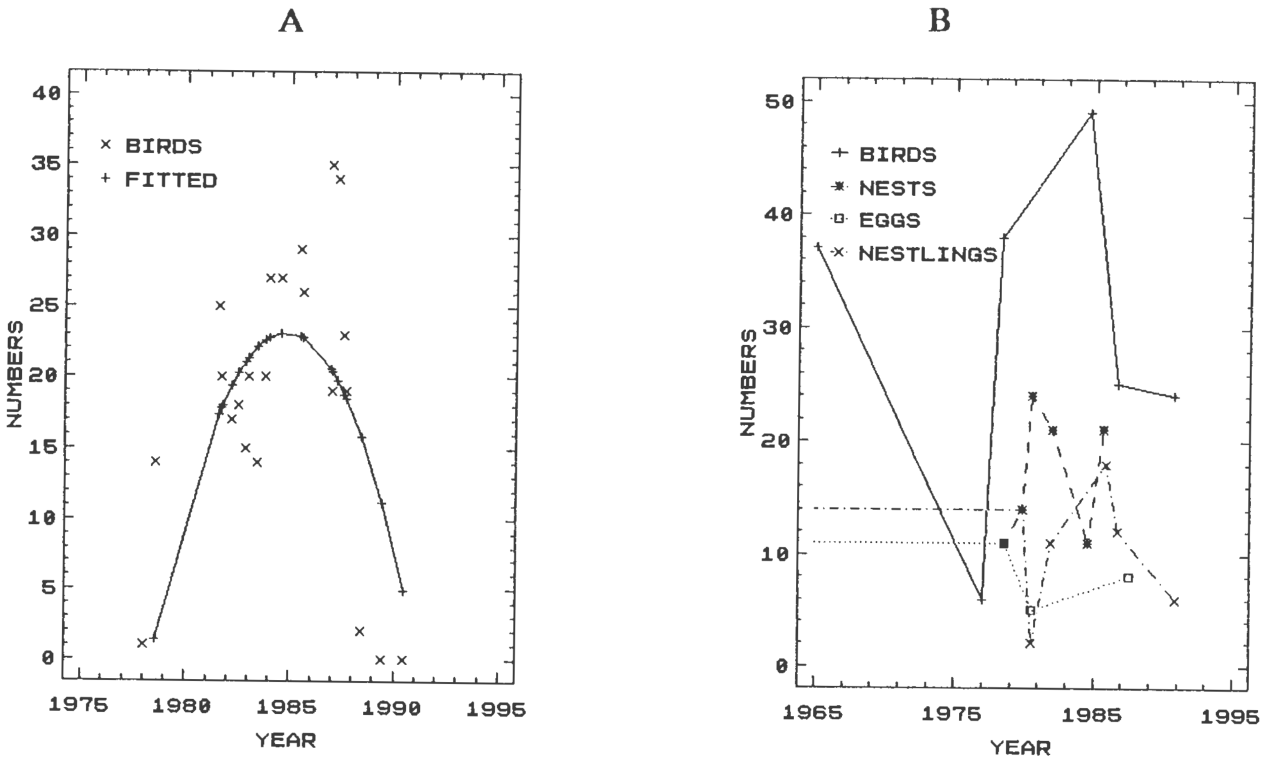

Figure 3.57 A. Aasvogelvlei (Site 8). Variation in the number of birds during the period 1978 to 1990, both years inclusive. B. Balloch (Site 10). Variation in the number of birds, nests, eggs and nestlings in the period 1965 to 1990, both years inclusive.

Trends at sites in the Cape Province

Consideration is given to four sites in the Cape Province, two of them from the southwestern Cape complex, the only group of sites in a winter rainfall region.

Aasvogelvlei, Site 8.

This site was established in the late 1970s and slowly increased to about 25 birds in the mid-1980s whence it declined to extinction by 1990s (Figure 3.57 B). After the 1987 breeding season Aasvogelvlei was abandoned as a breeding colony and Cape Vultures were subsequently to be found breeding at Platterug, Perdeberg, and Boschberg, all within a radius of 17.5 km of each other (Boshoff & Scott 1990).

Balloch, Site 10.

The site at Balloch is a satellite colony which seems to be stable, but with considerable fluctuations (Figure 3.57 B). Cape Vultures continued to breed at Balloch through to the 1990 breeding season, but only in small numbers (Boshoff 1990).

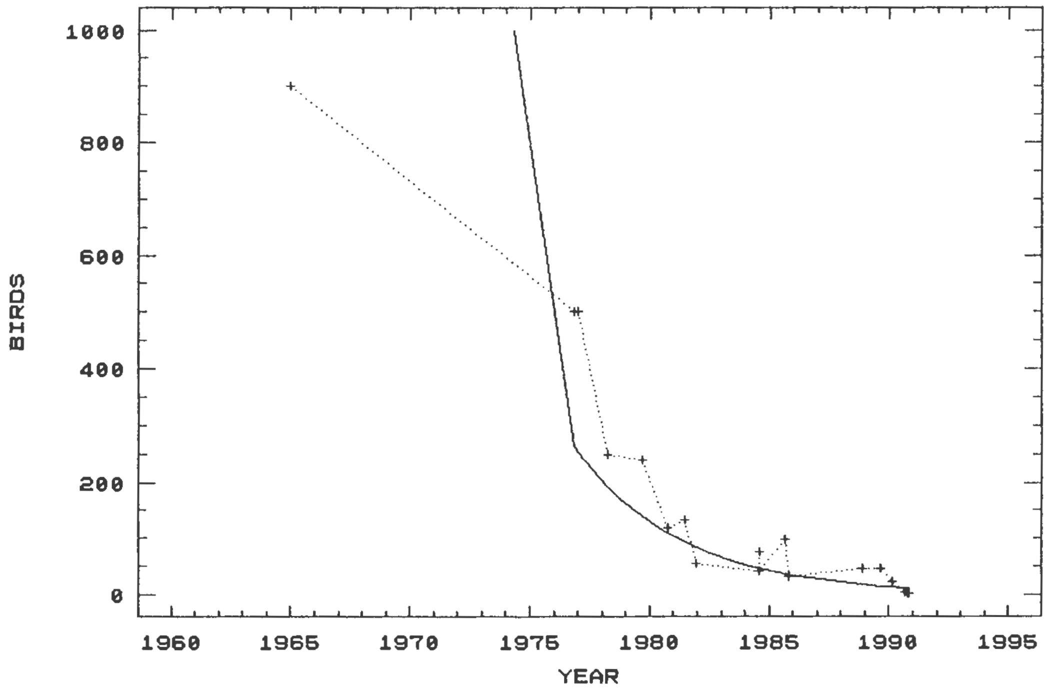

Figure 3.58 Karnmelkspruit (Site 31). Decline in the number of birds counted at the site during the period 1965 (estimated numbers) to 1986, both years inclusive.

Karnmelkspruit, Site 31.

The site at Karnmelkspruit was once a large and important breeding colony, about 900 birds were counted there in 1965 (Figure 3.58). From the local oral tradition the colony is thought to have persisted since the turn of the century (Boshoff & Vernon 1980a). Since the mid-1960s the population declined to about 500 birds in 1975 and decreased thereafter at about 22% p.a. The counts for the period 1976 to 1986 are considered reliable (Boshoff & Vernon 1987) and they clearly document the decline at this colony. It is thought that there were once 100 to 150 breeding pairs at this site (Boshoff 1990) but breeding ceased after the 1989 breeding season. Few birds have been seen at the colony since 1989 (loc. cit.). The reasons for the decline are given as (Boshoff 1990):

> "the widespread and indiscriminate use of poison by small-stock-farmers in the area; the poison is used to combat mammalian predators ... That many vultures have died from poison at or near the colony, and in the northeastern Cape in general, has been documented ...

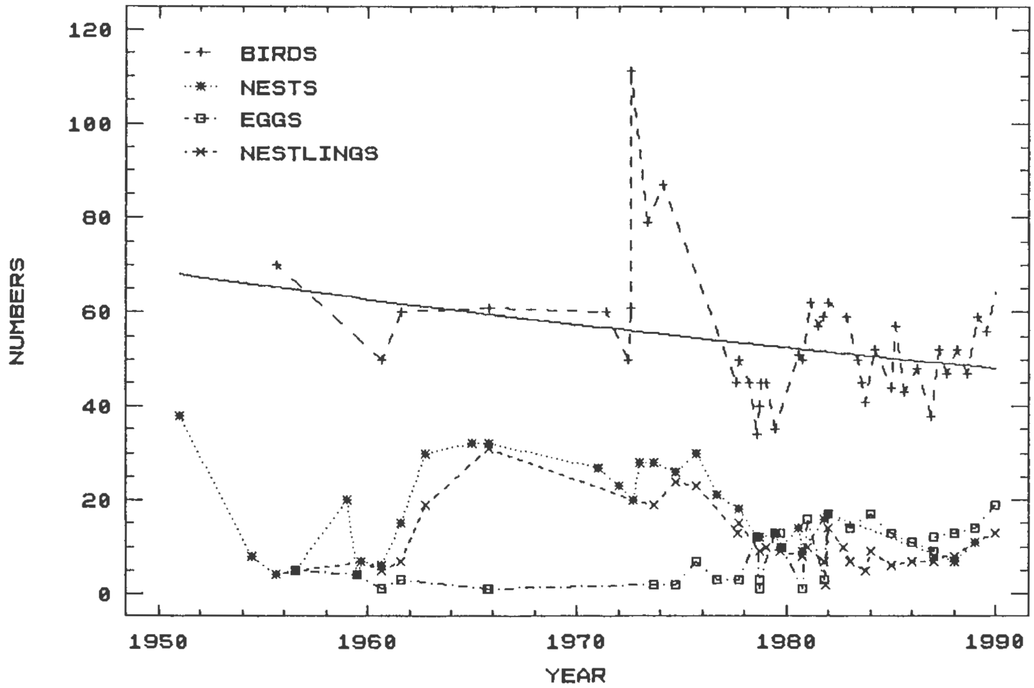

Figure 3.59 Potberg (Site 68). Variation in the number of birds, nests, eggs and nestlings in the period 1950 to 1990, both years inclusive.Data stored in the file.

Potberg, Site 68.

The first reliable census of the Potberg site was made in 1952 and the site was then visited from time to time until 1974 when regular visits were made each year for the purposes of ringing (Boshoff 1987). In the early 1980s there commenced an intensive study of the species' breeding biology (Robertson 1986). Since then the site has been subject to an annual census as part of the Cape Nature Conservation's routine monitoring programme (Boshoff & Scott 1990). The number of birds counted at the colony has shown much variation (Figure 3.59) but there has been a steady decline. Part of the variation is due to the regular interchange of birds between Potberg and the nearby Little Karoo range where a number of sites have been used sporadically for breeding and roosting. To overcome the variation induced by local movements counts have been made simultaneously at both Potberg and in the Little Karoo (i.e. on the same evening). These have tended confirm the inter-site transfers. The breeding data-set for the period 1974 to 1990 is particularly good and is to be used as the basis for a population modelling exercise. It will be shown that the annual productivity, as measured by large nestlings alive at the end of the breeding season, has remained constant over the period 1974 to 1990, both years inclusive (see section 7.2 below).

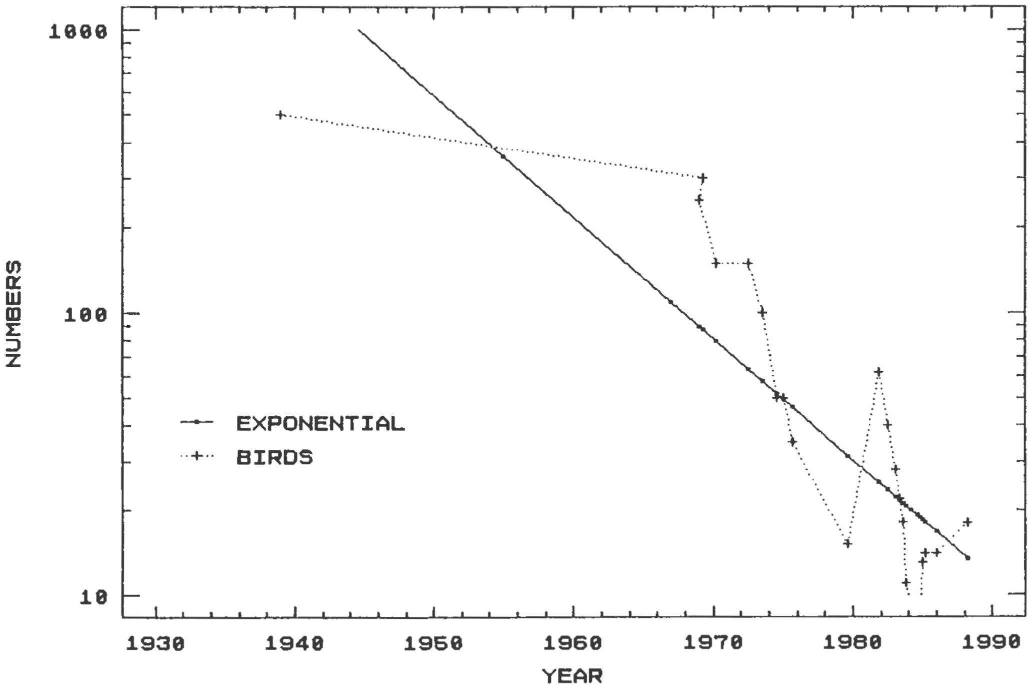

Figure 3.60 Waterberg (Site 100). Decrease in the number of birds counted during the period 1939 (early numbers are crude estimates) to 1988, both years inclusive.

Trends at sites in Namibia.

There is only one extant site in Namibia, all the other known sites were abandoned some time in the period 1950 to 1970.

Waterberg, Site 100

The site at Waterberg in Namibia has declined, with only one reversal, in the period 1939 to 1984 (Figure 3.60). Although the early counts are crude estimates, the numbers there were so large that the roughness of the counts does not detract from their validity. Some of the persons who made those early counts have been interviewed in recent times and are willing to confirm them (C.J. Brown pers. comm, pers. obs.). The rate of decline is estimated at 9.4% p.a. and has been attributed to the joint effects of deliberate poisoning and bush encroachment as a consequence of overgrazing (Brown 1985). The decline at this colony is matched by an overall decrease in Cape Vultures in Namibia and the abandonment of all other sites known to function since 1950. In addition, there have no recent Cape Vulture recoveries in Namibia of birds ringed in the Transvaal, whereas there were four in earlier times (see Chapter Five for details).

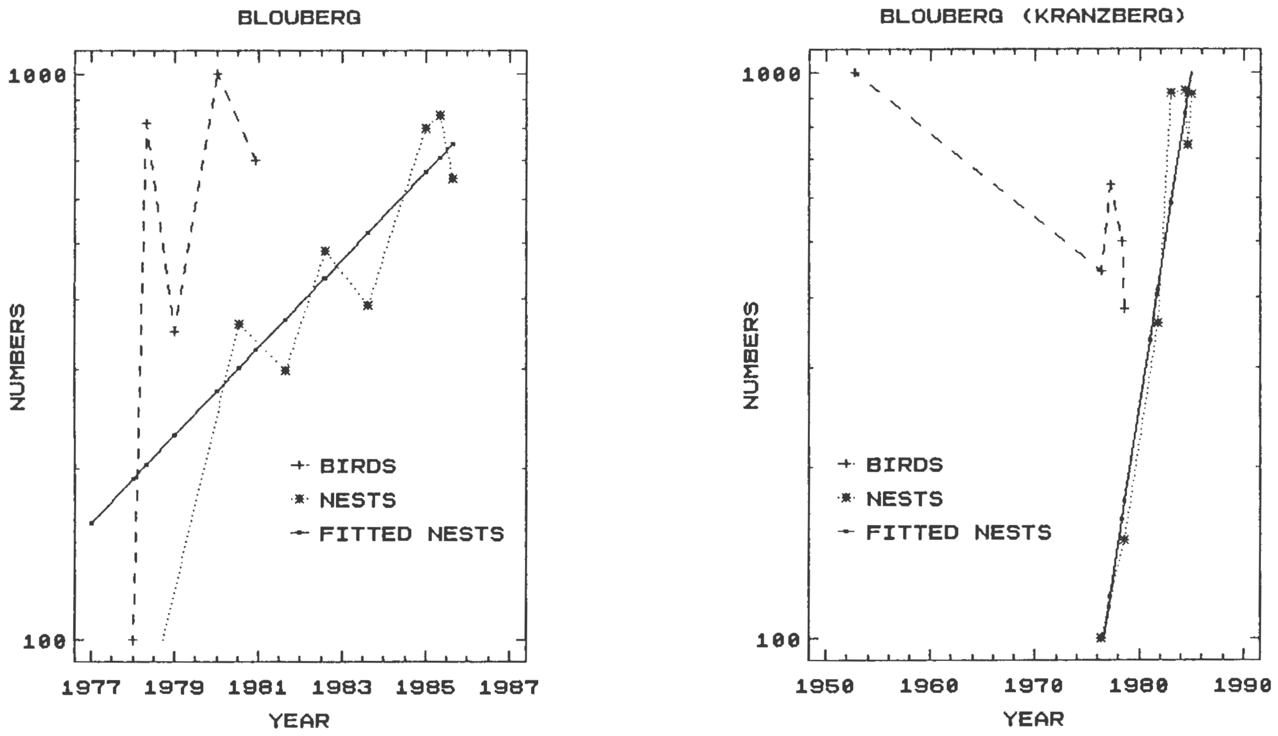

Figure 3.61 A. Blouberg (Site 12). Number of birds counted and the increase in the number of active nests estimated. B. Groothoek (Site 33). Number of birds counted and the increase in the number of active nests estimated.

Trends at sites in the Transvaal

Of the five Transvaal sites to be discussed below data for three of them (i.e. Blouberg, Groothoek = Kranzberg and Manoutsa) come largely from the interim reports issued by the team based at the Nature Conservation Division of the Transvaal Provincial Administration. They used a technique based on aerial photographs (taken from a helicopter) and it is now clear that the earlier estimates of active nests at each colony were negatively biased (Benson, Tarboton, Allan & Dobbs 1990). After a careful study of the various biases 'best estimates' have been made which suggest that there have not been any trends in active nests at these three colonies, rather there has been an improvement in the counting technique (loc. cit.).

Blouberg, Site 12

This is one of the largest Cape Vulture colonies. The estimated number of 'sites used' varied from 771 to 856 for the period 1980 to 1985 (Benson, Tarboton, Allan & Dobbs 1990: 137). The growth in nests (Figure 3.61 A) is thus not real. There is evidence of poisoning and persecution in the region around this site.

Groothoek, Site 33

Another extremely large Cape Vulture breeding colony for which the 'sites used' were estimated to vary between 787 and 967 for the period 1981 to 1985 (loc. cit.). There is a Post Office telecommunications tower atop this site which is a source of mortality, especially for young birds.

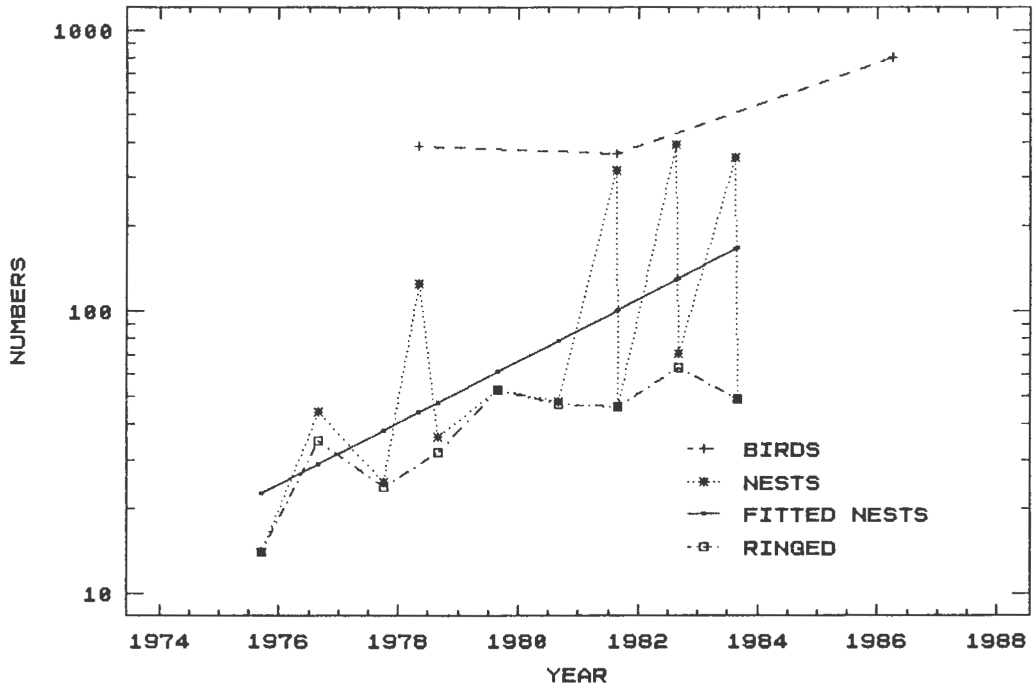

Figure 3.62 Manoutsa (Site 33). Number of birds and nests counted and the numbers of nestlings ringed.

Manoutsa, Site 45

This large colony is almost at the eastern edge of the species range in the Transvaal and it is likely that many of the adult Cape Vultures seen in the Kruger National Park come from this colony (see patterns of recoveries and resightings in Chapter Five). This colony would seem to be growing but the numbers of 'active sites' were estimated to lie between 660 and 733 for the years 1981 to 1985, both years inclusive (Benson, Tarboton, Allan & Dobbs 1990: 138): these estimates are based on aerial surveys. An incomplete ground census in 1985 yielded an estimate of 468 active sites - about 791 of the 905 potential sites were included in the ground census (i.e. 87.4%). Multiplying up the estimate of 468 by 1/0.874 = 535 which is to be compared with the aerial census estimate of 660. A difference of about 23% which seems large even allowing for the 19% 'failure correction factor' (loc. cit.).

Roberts' Farm, Site 72

There has been some variation in the number of nests and nestlings counted at this site (Figure 3.63 A). There is no statistically significant trend at this colony, but this may be reflection of variation in counting methods used. In the late 1980s a strong decrease in the number of nests was noted (Verdoorn, Becker & Branfield 1992: 27 ff.).

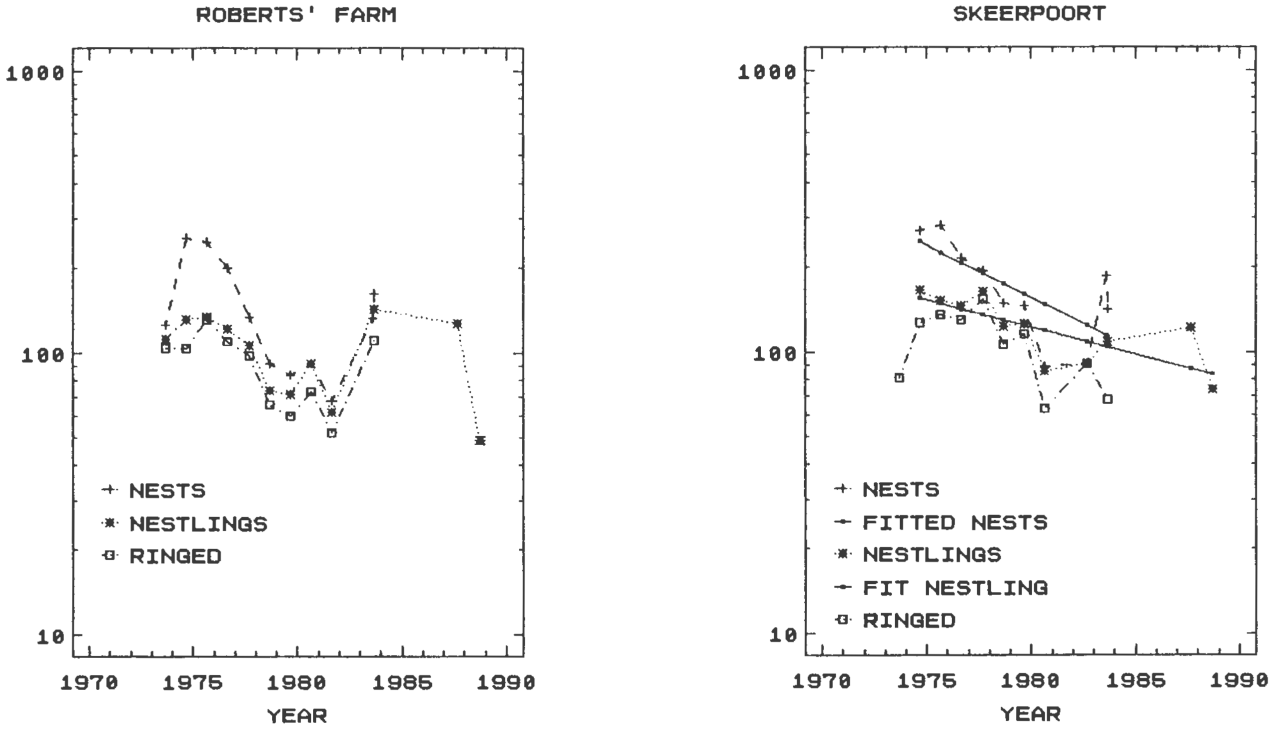

Figure 3.63 A. Roberts' Farm (Site 72). Numbers of birds and nests counted and the numbers of nestlings ringed. B. Skeerpoort (Site 79). Numbers of nests and nestlings counted and the number of nestlings ringed.

Skeerpoort, Site 79

Skeerpoort is along the same mountain range as its sister colony Roberts' Farm but it is much closer to the sprawling Pretoria and Johannesburg urban areas and so suffers more from direct and indirect persecution. Many 'day-trippers' visit the area, there is a major road along the foot of the colony which carries a heavy (and noisy) traffic load and many light aircraft and helicopters pass overhead, often too low. The colony showed a decline in the number of active nests and nestlings produced during the period 1973 to 1989. However, the number of active nests increased appreciable to 109 in 1989 (Verdoorn, Becker & Branfield 1992: 26).

Summary

Of the about 167 active Cape Vulture sites only 14, i.e. less than 9%, have sufficient temporal data from which to make some assessment of the trends in attendance, breeding or productivity. This is most unfortunate because it makes it difficult, if not impossible, to provide any overall measures of change in the population as a whole. It also means that it is impossible to provide adequate answers to the questions posed at the start of this section. In the following chapters a number of attempts will be made to answer some of these questions, but using data from other sources.

3.4 Summary

The total population size is put at 12 000 birds and about 4400 breeding pairs. This estimate is higher than any other ever published and reflects the more complete census and literature search conducted for the Site Register (Piper, Mundy & Vernon in prep.). About 55% of these birds and 68% of all breeding pairs may be found in the Transvaal and Botswana, which together function as a single unit. A second and smaller grouping is to be found in the Transkei, Lesotho and Natal which together have about 33% of the birds and 30% of the breeding pairs.

The current data-sets do not permit any conclusions to be drawn concerning the proportion of birds in any given age class. As a surrogate, it is necessary to use the proportion of non-breeding birds. The proportion of birds which are breeding is lowest in the Orange Free State, Natal and the Cape, all at less than 40% and highest in Botswana, Lesotho and the Transvaal, all at greater than 70%. It is also noted that larger sites have higher proportions of breeding birds, but this may be an artifact of the census methods used. The concentrations of non-breeders, measured in absolute numbers, is highest along the Natal/Lesotho border, in the northwest Transvaal and northeast Botswana and in Zimbabwe. The highest proportions of non-breeders are in the eastern Cape, O.F.S./Natal and in Zimbabwe, all of which are suspected of being ‘nursery areas’ (see Chapter Six below).

The sightings data from SABAP were used to construct distribution maps via the reporting rate. These maps agreed in large measure with those from the Site Register count data, except in the following areas.

1) There were concentrations of sightings of the Cape Vulture in the Kruger National Park, central Transvaal, northern Natal (mainly in or near the Zululand conservation areas), central Karoo, Kalahari Gemsbok National Park and northern Cape. In none of these areas is there a known, active roost. In fact, in most of them there is not even a suitable cliff site. This suggests that there are areas used by Cape Vultures in which they probably roost on trees or on power transmission structures. In a survey of the Dronfield

Ranch area (near Kimberley, northern Cape) it was found that Cape Vultures did just this (Mundy 1982) - this area was suggested as a 'nursery area' (see Chapter Six below). Thus it may be suggested that those Cape Vultures not tied to a breeding colony may wander into and use areas where there is food but where there are no suitable cliffs for roosting, provided there are trees or other structures on which they can overnight.

2) Using the 'point spread functions' to distribute Cape Vultures out over the plane creates a zone around each site, or group of sites. It is seen that whatever radius is used to maximize the geographical match between the colony and SABAP data-sets ends up with a zone-of-influence which is too large (Figure 3.48). This may be because no cognizance is taken of the habitat. It is likely that certain habitats and land-use practices (e.g. large open water-bodies, urban, forestry and large-scale cultivation) are totally inimical to the Cape Vulture. Thus when constructing models of home range and habitat use the nature of the terrain and the human activities on it must be taken into account.

The sightings data from SABAP have been treated as error-free, but it is possible that some of the unusual sightings could have been misidentified African Whitebacked Vultures. The SABAP breeding data are too sparse and inaccurate to be of any use and there were insufficient sightings data across all months to permit adequate testing for seasonality[1].

It was possible to elucidate the trends in attendance at 14 sites. Those sites found to be decreasing tended to be at the edge of the species' range while those sites which are stable or increasing are in the core areas.

The use of two independent data-sets (Site Register and SABAP) for mapping the spatial distribution of the Cape Vulture has shown that its spatial component is now know to a greater accuracy than ever before. However, the way the population is changing in space and time is less well known and requires further study.

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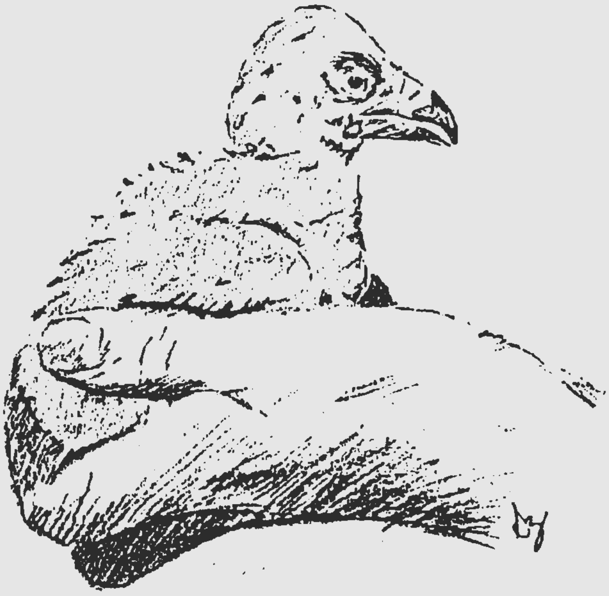
[1] This is no longer true, recent research by the SABAP team has shown that there is some slight variation in reporting rate, see the footnote on page 103.



Chapter Four

Fecundity

Contents Page

Abstract

To model the growth of a population it is necessary to estimate the number of new individuals entering the population each year, i.e. its productivity. Productivity is a function of the total number of individuals in the population which are capable of breeding, the proportion which actually attempt to breed and their subsequent breeding success. Estimates of breeding success are collated for the Cape Vulture from various breeding colonies, and comparative data are collected from other species. There are two Cape Vulture breeding colonies for which there is at least ten years of continuous data (i.e. Colleywobbles and the south west Cape) from which to estimate the components of fecundity. From these data it is suggested that the likely maximum proportion of adults which breed is about 85%, and the maximum egg to large nestling productivity is 75%. Thus the fecundity, measured as large nestlings per adult pair p.a. is likely to be, at most 0.64, i.e. 0.32 females per female p.a. This means that it takes an average of at least 3.14 breeding seasons for a female to produce a large female nestling. The total number of breeding pairs is estimated to be 4400 and so the maximum annual output of large nestlings will be less than about 2800.

Chapter Four

Fecundity

The study of breeding is crucial to demography. Breeding is the source of new individuals to the population. The maximum rate at which new individuals can be generated sets an upper limit to the rate at which a population can grow. Fecundity is defined, in these researches, as the rate at which a female, capable of breeding, can produce new females each year. There are three important components of productivity: the total number of individuals who are capable of breeding, the proportion who do attempt to breed, and their subsequent breeding success. Breeding success is measured as the ratio of nestlings alive on 15 September to number of eggs laid.

From a comparison of other K-selected[1] birds, e.g. Old and New World vultures and large seabirds, it is to be expected that the Cape Vulture will be characterized by an extremely low fecundity (see review by Amadon 1964) and a concomitantly high survival rate (see analysis of California Condor, Mertz 1971). From the data presented later in this chapter, it will be shown that the maximum fecundity will be about 0.32 female nestlings per adult female, p.a. This means that it will take at least 3.125 years for a female to produce a large female nestling. This compares with Abbott's Booby *Sula abbotti* for which it has been shown (Nelson & Powell 1986) that pairs rear one fledgling (of either sex) every 5.1 years and take 23.8 years to replace themselves.

This chapter is divided into three parts. First, consideration is given to the number of individuals capable of breeding and the proportion which actually breed. Secondly, comparisons will be made between species of similar demography to obtain estimates of the range of values within which productivity should lie for a bird of the Cape Vulture's size and life history. Thirdly, the data from two breeding colonies will be examined in detail to provide estimates of each of the components of fecundity.

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[1] For a definition of the terms r- and K-selection consult MacArthur & Wilson 1967; see also the description in Horn & Rubinstein 1984: 284 ff.

4.1 Number of breeding pairs

The factors regulating breeding in the Cape Vulture have been examined by Vernon & Robertson (1982), and the following sections draw on their review. Throughout this discussion, no distinction will be made between 'breeding pairs' and 'breeding females' because Cape Vultures form monogamous pairs and both parents need to be present in the early part of the breeding season to protect the egg or small nestling (Robertson 1982). Thereafter they are both needed to provision the single youngster (Komen 1984, 1986). While Cape Vultures seem to be completely monogamous, and extra-pair copulations (EPC) and forced extra-pair copulations (FEPC - a euphemism for rape) do take place (Robertson 1986), it is unlikely (in my opinion) that this has any major effect on the population dynamics.

It may be possible to dispense with an estimate of the proportion of sexually mature birds which breed, because it is possible to count the number of breeding birds directly (see Chapter 3 above). Using the analyses from the previous Chapter it is possible to sketch the variation in the number of breeding Cape Vultures, both in space (section 4.1.1, below) and with time (section 4.1.2, below). Knowing the space-time distribution of the number of breeding pairs is sufficient for modelling productivity and it is not necessary to have an estimate of the proportion who do not breed. But, when the population is examined 'as a whole', it is important to know how many birds are not breeding.

Breeding may also be looked at from the point of view of the individual rather than of the population as a whole, in which case it is necessary to consider the individual's lifetime reproductive success (LRS, *sensu* Newton 1989). The components of LRS are number of breeding seasons, number of broods p.a. and brood size (Newton 1989: 447 ff.). For the Cape Vulture, the number of broods p.a. is fixed at one (it takes nearly nine months to complete the breeding cycle) and the brood size has a maximum of one (the clutch size is usually one, only one double clutch is known to have produced viable nestlings, Vernon & Piper 1986). Thus the only component with the potential for variation of any magnitude, is the number of breeding seasons. The number of breeding seasons is in turn a function of the age at first breeding, the number of years over which the individual breeds and the timing of senescence.

Birds that do not breed in any one year can be categorized into three groups: those that have not yet started to breed, those that have temporarily suspended breeding, and those who have ceased to breed. This classification differs slightly from that advanced by Vernon & Robertson (1982), whose suggested divisions are "birds competing for breeding sites, birds with sites but not breeding, and birds which are breeding". The age at first breeding is examined in section 4.1.3, the proportion which breed is discussed in section 4.1.4 and the age-specific proportion of breeders is elaborated upon in section 4.1.5 below.

4.1.1 Spatial variation in breeding pairs

The number of breeding pairs of Cape Vultures can be readily estimated early in the breeding season by counting the number of active nests at each colony. The data from these counts have been collated into a single data set (see section 3.1.1, above) and used to estimate the density distribution of breeding pairs (see Figure 3.23). For the purposes of this section, point estimates, rather than spatially smoothed density estimates, are required. The same colony breeding data, as have been used before, are now portrayed as discs. The radius of the disc, R, is proportional to the square root of the number of breeding pairs (Figure 4.1). Thus the area of the disc (i.e. πR^2) is directly proportional to the number of breeding pairs; a disc with twice the area will look twice as big and will represent twice as many birds.

The conclusions to be drawn from this map (i.e. Figure 4.1) are similar to those presented earlier (section 3.1.1, above).

1) There is a high concentration of breeding pairs at sites in the Transvaal and Botswana.
2) There is a great concentration of small sites in Natal, Lesotho, the northern Cape and Transkei, associated with a few larger sites.
3) The south-western Cape has two isolated small colonies.
4) There is a single, isolated site in Namibia.

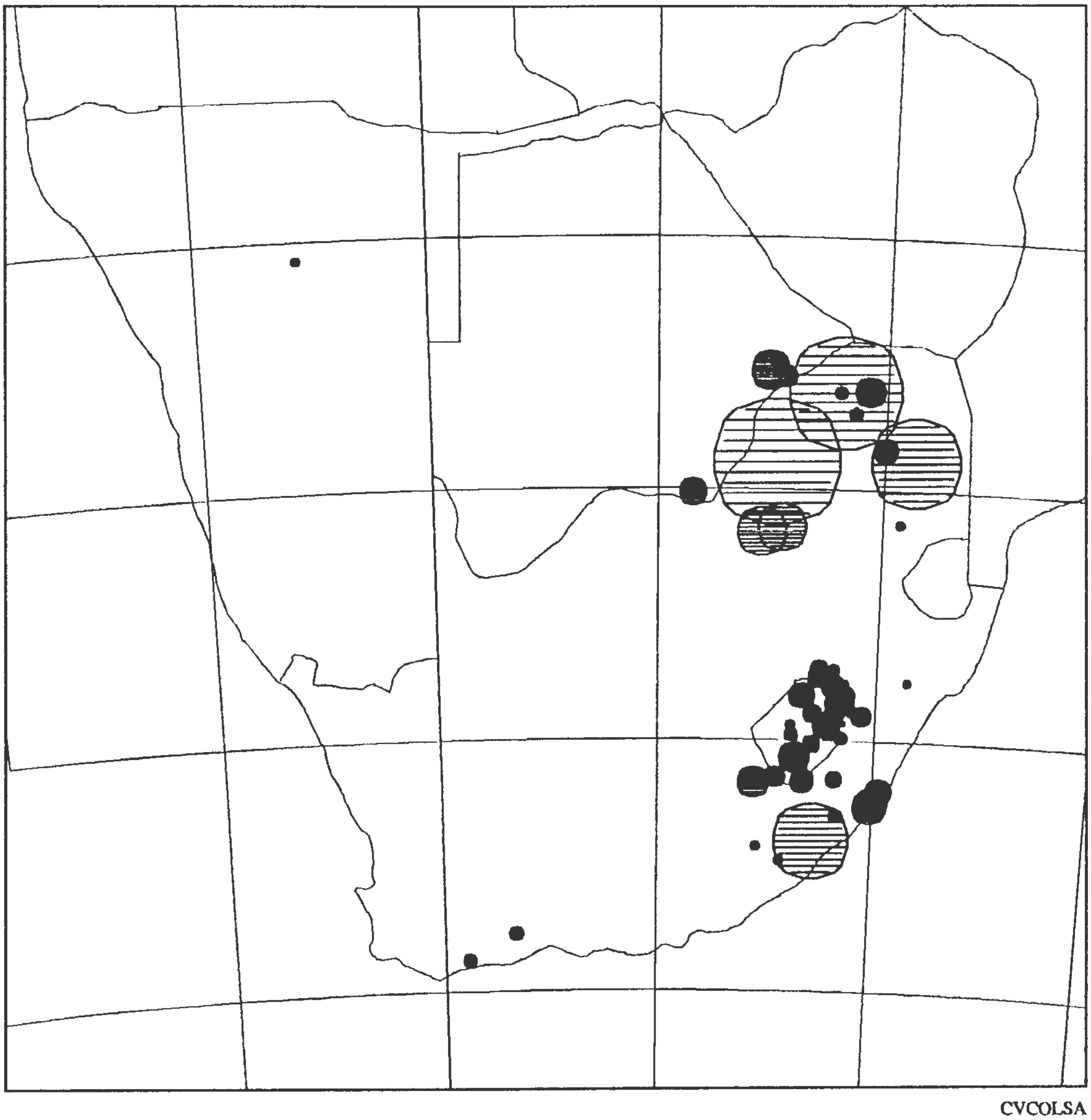

Figure 4.1 Location and size of Cape Vulture breeding colonies. Centre of circular disc is placed at colony location and radius of disc is proportional to the square root of the number of breeding pairs. The biggest disc shown represents about 1000 breeding pairs.

4.1.2 Temporal variation in breeding pairs

Using the data of sections 3.1.1 and 3.3 above, it is possible to extract three sub-sets of data: one list each for those breeding colonies which have decreasing numbers of breeding pairs (Table 4.1), those which are stable (Table 4.2), and those which are increasing (Table 4.3). These data may also be displayed on a locality map of southern Africa (see Figure 3.10, above), from which it may be seen that all but one of the breeding colonies which are increasing, are to be found in the Transvaal and Botswana.

Table 4.1
List of colonies which have a decreasing number of breeding pairs.
(No. of pairs as at last count: see section 3.1 above.)

Site	*Name*	*Pairs*
8	Aasvogelvlei	11 [1]
15	Forest Range	5 [2]
31	Karnmelkspruit	58 [3]
35	Ku-Yeneni	10
39	Bonwalenong	82
44	Mannyelanong	44
68	Potberg	10
77	Semonkong	10
79	Skeerpoort	140
85	Kukubye	30
176	Sehonghong River	5

Table 4.2
List of colonies which have a stable number of breeding pairs.
(No. of pairs as at last count: see section 3.1 above.)

Site	*Name*	*Pairs*
10	Balloch	25
18	Colleywobbles	350
50	Mechachaneng	25
67	Vulture's Peak	30
72	Roberts' Farm	145
83	Thaba-Tseka	20
89	Umtamvuna	40
90	Mtentu	60
91	Quthing Valley,Upper	55
164	Mtzikaba	65
179	Metebong-ea-lelingoa	10
300	Mara, Zoutpansberg	55
305	Loskop	10
311	Weltevreden	5
313	Bolahla	10
318	Lower Moremoholo	25

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[1] Site now abandoned, Boshoff & Scott (1990).

[2] Site now abandoned, C.J. Vernon pers. comm.

[3] Site now abandoned, C.J. Vernon pers. comm.

There is a triplet of colonies in the Tswapong Hills of Botswana, one of which is increasing while the other two are decreasing. This may well be a case of colony-switching as a result of disturbance at the two sites which are decreasing (see section 3.3 above). There is one site in Namibia which is increasing. This site (Waterberg), now greatly diminished (see section 3.3, above), is showing signs of recovery and this is due entirely to the conservation action of the local authorities (C.J. Brown pers. comm.).

There are three central Transvaal sites (Blouberg, Groothoek and Manoutsa) which are said to be increasing. However, the censuses carried out at these colonies in the 1980s were based on the newly developed aerial census method and the increases noted may be a reflection of an improvement in the use of the technique rather than an increase in the number of birds (Benson, Allan, Tarboton & Dobbs 1990; see also section 3.3 above).

More than three-quarters of the sites which are decreasing are on the edge of the species range, or are isolated sites. Thus this may be evidence of range contraction. Other evidence for range contraction is to be presented in Chapter Six, below).

Table 4.3
List of colonies which have an increasing number of breeding pairs.
(No. of pairs as at last count: see section 3.1 above.)

Site	*Name*	*Pairs*
12	Blouberg	800
21	Manong Yeng	80
33	Groothoek	1000
45	Manoutsa	500
100	Waterberg	5 (after a previous decline)

4.1.3 Age at first breeding

It is likely that there will be considerable variation in the breeding performance between individuals of a population (Newton 1989: 449). The first step in quantifying this is to split the population up into pre-breeders and breeders and then to regard each of these two groups as internally homogeneous, with respect to breeding (Clobert & Lebreton 1991: 79). Unfortunately there are very few data on the age of first breeding of Cape Vultures. Thus it is important to turn to other species for comparative data (Table 4.4). The use of comparative data is motivated because it is now known that demographic parameters tend to respond in an allometric fashion to overall body size (Clobert & Lebreton 1991: 78). In particular the age at first breeding increases with increasing lifespan (Lack 1968: 295 ff., see also loc. cit. Table 29)

Table 4.4

Comparison of ages at which various species first breed.

			Age first breed		
Group	*Species*	*Sex*	*Mean*	*Range*	*Comment & Reference*
Raptors	European Sparrowhawk	F	2.0	1-4	Newton (1985)
	Osprey		3.1	3-6	Postupalsky (1989)
	Peregrine	F	2.0	1-5	Mearns & Newton (1984)
	Red Kite			2-7	Newton, Davis & Davis (1989)
	Ural Owl	F	4.0	1-9	Saurola (1989)
Vultures	Andean Condor			8	Lint (1960)
	California Condor	M		7	'Single male', Snyder, Snyder, Hamber & Cox (1985)
	Eurasian Griffon[4]			5-6	Mendelssohn & Leshem (1983)
				5-7	Glutz von Blotzheim *et al.* (1971)
				5-6	Mundy (1985: 471)
		F	5		'Single female', Terrasse (1977)
				4-5	Cramp & Simmons (1980:79)
	Cinereous Vulture		9		Mundy (1985: 471).
				5-6	Cramp & Simmons (1980: 94)
	Bearded Vulture			5+	Cramp & Simmons (1980: 62)
	Egyptian Vulture			4-5	Cramp & Simmons (1980: 69)
	Lappetfaced Vulture			4-5+	Cramp & Simmons (1980: 87)
Seabirds	Kittiwake	M	4.7		Woller & Coulson (1977) and Coulson (1988)
		F	5.1		
	Fulmar		8.0	6-19	Ollason & Dunnet (1988)
	Shorttailed Shearwater		7.0	4-15	Wooller, Bradley, Skira & Serventy (1989)
	Redbilled Gull	M	3.3	2-5	Mills (1989)
		F	4.2	2-6	
	Adélie Penguin	M	6.2	4-8	Ainley, Le Resche & Sladen (1983)
		F	4.9	3-7	
	Wandering Albatross	M	12.1	9-16	Weimerskirch & Jouventin (1987)

If the comparative data for age at first breeding (Table 4.4) are a reliable guide then the Cape Vulture should commence breeding at between 5 and 7 years of age. However, it should be born in mind that some of these data come from captive breeding studies or from observations of healthy wild populations and so are likely to provide optimistic estimates of the age at first breeding (D.C. Houston, pers. comm.). In those demes of the Cape Vulture which are in poorer habitats the age at first breeding could be higher.

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[4] Additional data for this and the next four species were published after the completion of this chapter: Mundy, Butchart, Ledger and Piper 1982.

In general, in larger species, individuals will tend to breed some years after 'physiological maturity, when gonads first become functional' (Newton 1989: 452). For the African Whitebacked Vulture *Gyps africanus* it was found that 11.7% of breeders were in the age category 'immature' (i.e. less than 4 years old), 15.3% were sub-adult (about 4-5 years old) and 73% were adult (5 years and older; Mundy 1982: 156, Table 44 for Zimbabwe 1973-1975 and Kimberley 1975). In my opinion, the major constraint likely to inhibit early breeding in the Cape Vulture is food availability. This is because it is currently unlikely that the other two factors preventing breeding (i.e. availability of nest sites and mates, Newton 1989: 452) will be operational[5]. During the 1980s the number of breeding birds at Main Cliff, Colleywobbles increased steadily (see section 4.3.1 below) but from 1988 the numbers decreased. By 1991 they were at the lowest they had been in nearly a decade and it was noted that the number of sub-adult birds in and around the breeding cliffs had increased (C.J. Vernon, pers. comm.). I therefore suspect that as the number of mature adult birds dropped below some critical level younger birds were able to come in and breed.

For the Cape Vulture there are only three reliable records of known age birds breeding[6]. At Potberg, a male colour-ringed Cape Vulture was into its seventh year and it paired and bred successfully with a female, also colour-ringed who was into its fifth year (Robertson 1983). A captive Cape Vulture made an unsuccessful breeding attempt in its sixth year (Mundy 1982: 267). While it is hypothesized that Cape Vultures attain their adult plumage at about six years (Piper, Mundy & Vernon 1989) it is not possible to be certain of this. However, there are some data on the proportions of sub-adult birds breeding. Of all the Cape Vultures breeding at Potberg during 1981 and 1982, two were not adults out of totals of 34 and 36, constituting 5.8% and 5.5% respectively (Robertson 1983: 96). In the Magaliesberg during the years 1973 to 1975 it was estimated that two of 38 breeding birds were sub-adult, i.e. 5.3% (Mundy 1982: 192).

4.1.4 Proportion of adults which breed

As a second step in modelling individual variation in reproductive performance, the population of birds which have reached the age of first breeding can be split into breeders and non-breeders. This is possible because it has been observed that (Newton 1989: 452-453, and references therein):

> Non-breeding years among established breeders are clearly frequent in species subject to annual fluctuations in conditions ... They are also regular in long-lived species subject to more stable conditions.

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[5] It has been suggested that there could also be social constraints operating to inhibit breeding (E. Danchin, pers. comm.). As yet, no studies have been undertaken of the social factors which come into play during breeding in the Cape Vulture.

[6] During the 1992 breeding season there were eight known-age birds breeding at Potberg - these data are still to be published: A.F. Boshoff pers. comm.

Table 4.5

Comparison across species of proportions of adults which breed.

Species	*Era*	*Place*	*Proportion*	*Sample, comment & reference*
African Whitebacked Vulture	1973-1975	Zimbabwe	0.867	211 - Mundy (1982: 157)
Hooded Vulture	1973-1975	Zimbabwe	0.78	19 - Mundy (1982: 229)
Cape Vulture	1973-1975	Magaliesberg	0.814	199 - Mundy (1982: 197)
	1981	Potberg	0.79	43 - Robertson (1983: 96)
	1982	Potberg	0.90	40 - ditto
	1985	Potberg	0.73	44 - Boshoff & Scott (1990: 35)
	1986	Potberg	0.49	45 - Ditto
	1987	Potberg	0.78	41 - Ditto
	1988	Potberg	0.76	45 - Ditto
	1989	Potberg	0.72	53 - Ditto
	1990	Potberg	0.89	54 - Ditto
	1988	Platterug	0.70	37 - Ditto
Eurasian Griffon	1979	Iberia	0.70	Total population estimated at 9250 individuals of which there are 3240 breeding pairs - Purroy (1981)
Lappetfaced Vulture	1973-1975	Zimbabwe	0.76	42 - Mundy (1982: 229)
Whiteheaded Vulture	1973-1975	Zimbabwe	0.82	17 - Mundy (1982: 229)
Palmnut Vulture			0.90	By implication, sample size not given - Thiollay (1976)
Shorttailed Shearwater	1947-1987	Fisher Island	0.88	Ca. 470 - Wooller, Bradley, Skira & Serventy (1989)

With respect to this demographic parameter there are some data available for the Cape Vulture and these are compared with data for a number of other species with similar demographic patterns (Table 4.5). From this comparison it would be reasonable to expect that the proportion of adults which breed, in a given year, is likely to lie between 0.7 and 0.9; in fact only one of the estimates for the Cape Vulture lies outside this range.

Most of the data for African vultures (i.e. in Table 4.5) come from estimates at nests and colonies and relate to those adults present there, but not breeding. What of the sexually mature Cape Vultures that are seen at roosts, often far removed from the nearest breeding colony? An estimate of the proportion of mature birds not at colonies needs to be made, but, there are currently no data which permit such an estimate to be made.

Finally, as a check on the realism of the estimate of the proportion of the total adult population actively breeding it is worth noting the estimate of 3240 breeding pairs Eurasian Griffons in a total Iberian population of 9250 adults (Purroy 1981). This yields a ratio of 0.70 (breeding birds to total) which is comparable with that of 0.73 for the Cape Vulture (from the previous Chapter - 4400*2/12000).

4.1.5 Age-specific proportion of breeders

There is considerable individual variation in productivity among breeding birds. Furthermore, individual variation can be summarized with respect to age and time. Enough comparative data have now been collected for Newton (1989: 458, 460) to assert that:

> Both survival and breeding success are age-dependent in birds, usually improving in the early years of life, and, at least in some species, deteriorating thereafter ... Deterioration of performance in later life, in the face of greater experience, can only be put down to senescence: to general wear and tear, which reduces efficiency and social status ... Improvements in mean performance may be apparent over only one or a few years in short-lived species ... but up to 9 years after first breeding in long-lived species ... Declines in performance in later life, extending over several years, have been noted ... Changes are commonly apparent in certain components of reproduction, such as laying date, egg size and clutch size, but are less often evident in production of young ... individuals do indeed perform progressively better in each succeeding year of early life.

For the Eurasian Griffon studied in the Pyrenees, Elosegi (1987) reported that:

> In one colony of about 30 pairs, a few have had remarkable success: the best raised 11 youngsters in 11 years at one nest site.

Methods have been suggested for testing for individual variation (e.g. Hatch 1988) but these have yet to be applied to any vulture species. In a detailed and long-term study of marked Eider Ducks (Coulson 1984) it has been shown that adult survival remained fairly constant over many years and over much change in the population size. Ducks were found to 'skip' a breeding season when in poor condition. Furthermore, it was found that breeding responded in a density dependent manner, with smaller clutch sizes and more missed seasons at higher densities.

Of the four components of breeding (i.e. laying date, egg size, clutch size and production of young) hypothesized to vary with age, one - clutch size - is not applicable to the Cape Vulture, one is not measurable - egg size (because of disturbance, see Vernon, Piper and Schultz 1984: 122) - while the other two are indeed amenable to measurement - laying date and productivity. In forthcoming two sections these will be analyzed. However, so few observations have been made of known-age birds that it is not possible to elucidate any age-specific variations in these parameters.

4.2 Productivity

Productivity is defined as the rate at which newly laid eggs result in large nestlings. Numerically, productivity is measured as young produced per breeding pair p.a. These two definitions are equivalent for the Cape Vulture because the clutch size is invariably one and there is, at most, one brood annually.

Productivity is a topic which has been exhaustively studied and for which there is a vast literature. Three approaches are used here to estimate productivity. First, a comparison is made across vulture species with similar life styles to that of the Cape Vulture, so as to set 'reasonable bounds' on productivity (section 4.2.1). Secondly, all published Cape Vulture productivity data are collated and compared (section 4.2.2). Lastly, reliable observations of productivity at two colonies are subjected to statistical analysis (sections 4.3.1 and 4.3.2).

Table 4.6

Comparison of productivity across a range of vulture species.

Species	*Era*	*Locality*	*Productivity*	*Sample, comments & reference*
Eurasian Griffon	?	?	0.66	33 - Abreu (1987)
	1972-	Pyrenees	0.70	Ca. 30 - Elosegi (1987)
	1982-	Pyrenees	0.7	61? - Leconte (1985)
		Italy	0.43	Ca. 20? - Schenk, Akesu & Serra (1987)
Rüppell's Griffon	1974-	West Africa	0.25	16=4 Nests over 4 years - Green (1977)
	?	East Africa	0.86	85 Eggs - Houston (1974)
African Whitebacked Vulture	1973-1975	Zimbabwe	0.60	171 - Mundy (1982: 157)
	1975	Kimberley	0.76	29 - ditto
Indian Whitebacked Vulture	1981	Dacca	0.57	7 Eggs gave 4 nestlings of which 2 flew - Sarker (1984)
Palmnut Vulture		Ivory Coast	0.67	12 - Thiollay (1976)
Bearded Vulture	1981	Corsica	0.33	6 Nests - Bouvet (1985)
	1960-1980	Pyrenees	0.76	85 Breeding attempts - Cheylan & Thibault (1981)
	?	Zoo	1.0	2 Pairs - Louwman (1981)
	1980-1982	Natal & Lesotho	0.89	18 Brown (1988)
Egyptian Vulture			1.29	14 Pairs - Abreu (1987)
	1979-1983	Provence	1.33	13 Pairs - Bergier (1985)
	1950-1980	Provence	1.3	59 Nests - Bergier & Cheylan (1980)
	?	?	0.81	141 Nests - Donázar & Ceballos (1988)

Table 4.6 (Continued)

Comparison of productivity across a range of vulture species.

Species	*Era*	*Locality*	*Productivity*	*Sample, comments & reference*
Hooded Vulture	?	Hwange	0.54	35 - Hustler & Howells (1988)
	1973-1975	Zimbabwe	0.40	15 - Mundy (1982: 229)
Lappetfaced Vulture	1973-1975	Zimbabwe	0.53	32 - Mundy (1982: 229)
	1972-1973	Serengeti	0.56	55 Eggs hatched 31 nestlings - Pennycuik (1976)
	1975	Zimbabwe	0.56	18 pairs - Anthony (1976)
Whiteheaded Vulture	1973-1975	Zimbabwe	0.57	14 - Mundy (1982: 229)
	1972-1973	Serengeti	0.5	8 Eggs hatched 4 nestlings Pennycuik (1976)
Cinereous Vulture	1972-1981	Mallorca	0.40	40 - Richford & Platt (1982)
	1975-1979	Cordoba	0.68	8 Pairs p.a. - Torres, Jordano & Villasants (1980)
California Condor	?	Zoo	0.80	15 eggs collected in wild, incubated in zoo - Kuehler & Witman (1988)
	?	Zoo	0.80	15 Eggs - Toone & Toone (1985)
	?	Zoo	0.80	Intensive care by zoo staff required - Snyder (1985)
	?	Wild	0.40-0.50	Snyder (1988)
Andean Condor	1966-1984	Zoo	1.00	18 Breeding attempts by same pair over 18 years - Johst (1986)
	1977-	Zoo	0.17	12 Eggs - Samour *et al.* (1984)
Turkey Vulture	1983	Pennsylvania	1.07	14 nests - Coleman & Fraser (1983)
	?	?	0.53	55 nests - Jackson (1983)
Black Vulture	?	?	0.38	49 nests - Jackson (1983)

4.2.1 Interspecific comparison of productivity

Productivity data from other vulture species have been summarized (Table 4.6). Productivity is measured as above (i.e. section 4.2), but it is important to note that many authors give no definition of their use of the term 'productivity'. It has been necessary to rework some data to make them roughly comparable.

Table 4.7
Comparison of Cape Vulture productivity across a range of colonies, eras and observers.

Era	*Locality*	*Productivity*	*Sample, comments & reference*
?	Magaliesberg	0.5	Anon. (1977)
?	Groothoek	0.85	77 - Undisturbed nests - Benson & Dobbs (1985)
?		0.67	11 - Disturbed nests - ditto
1984	Waterberg	0.75	4 eggs - Brown (1985)
1981	Kranzberg	0.47	17 eggs - Dobbs & Benson (1982)
1981	Kransberg	0.67	40 eggs - ditto
1985	Semongkong	0.71	14 nests - Donnay (1989)
1985	Lesotho	0.78	Unknown - Donnay (1989)
1962	Nooitgedacht	0.27	15 eggs to 4 fledglings - Houston (1974)
1982	Skeerpoort	0.44	50 - Komen (1985)
1973	Roberts'	0.52	23 - Ledger & Mundy (1973)
1973	Roberts'	0.56	32 - Mundy (1982: 193)
1974	Roberts'	0.67	33 - ditto
1975	Roberts'	0.71	24 - ditto
1975	Skeerpoort	0.67	27 - ditto
1974	Skeerpoort	0.94	116 - nestling survival, no fire, Mundy & Ledger (1975)
1974	Skeerpoort	0.81	70 - nestling survival- Fire - ditto
1977	Roberts'	0.79	135 - Mundy, Ledger & Friedman (1980)
1977	Skeerpoort	0.84	195 - ditto
1977	Mannyelanong	0.70	82 - ditto
1978	Roberts'	0.80	92 - ditto
1978	Skeerpoort	0.83	150 - ditto
1978	Mannyelanong	0.75	71 Nests found - ditto
1983	Mtamvuna	0.77	39 - Piper (1985)
1984	Mtamvuna	0.81	28 - ditto
1985	Mtentu	0.70	60 - Piper & Ruddel (1986)
1985	Mtzikaba	0.95	56 - ditto
1981	Bawa Falls	0.51	49 - Vernon (1982)
1981	K.M.S.*	0.54	56 Vernon, Boshoff & Robertson (1983)

* K.M.S. = Karnmelkspruit

An examination of these data reveals that the likely maximum limit on productivity is about 0.8 and the likely minimum limit is about 0.5. In arriving at the lower limit it is important to avoid estimates from small, isolated or declining populations. Also, it is necessary to remember that an estimate of productivity, which is a ratio, from a small sample will have much wider confidence limits than a similar one from a large sample. While an effort has been made to reduce these estimates to the same common base, it has not been possible to do so for all studies because the methods used to calculate productivity are not given for every study. In addition, what may seem to be species with similar life-history patterns may in fact differ markedly (E. Danchin, pers. comm.).

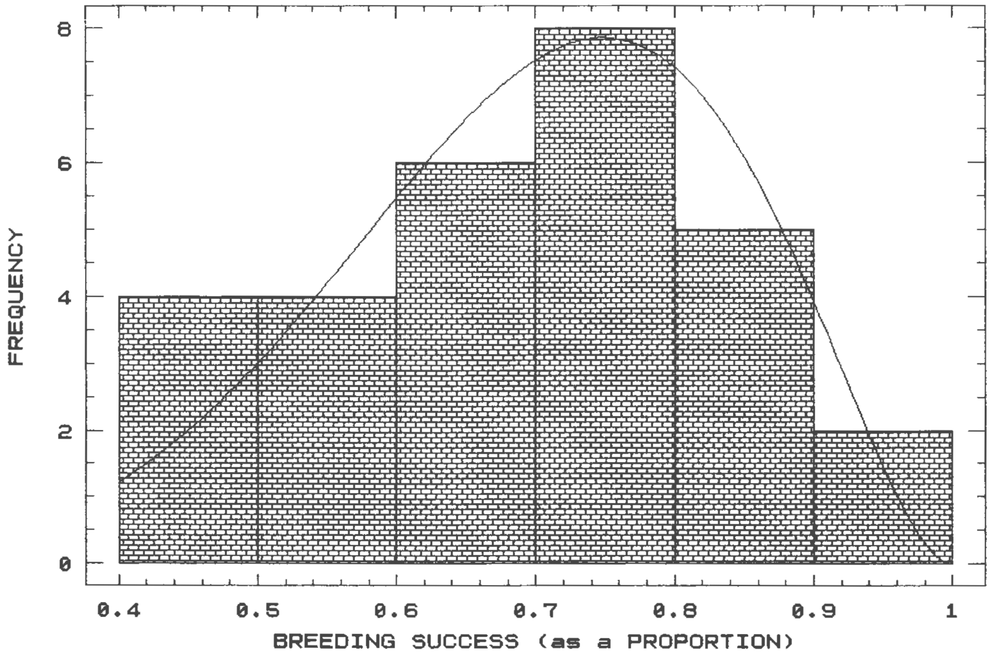


Figure 4.2 Distribution of 29 breeding success values extracted from the literature on the Cape Vulture.

4.2.2 Intraspecific comparison of productivity

The published records of Cape Vulture breeding have been collated and summarized (Table 4.7). Where possible, records have been recomputed so that productivity is measured as large nestlings produced per breeding pair p.a.

The breeding success figures extracted from the literature may constitute a random, nor a representative sample because of the following reasons.

1) Not all the breeding colonies have been sampled.
2) The samples used are not randomly drawn from the colonies studied.
3) The same data may reappear in two, or more, of the entries.
4) Not all workers have used the same methods.

Notwithstanding this, the breeding success data show a reasonable distribution (Figure 4.2) lying between 44% and 95% with 10 and 90 percentiles of 47% and 85%. The quartiles are 56% and 80%. The mean is about 70% and the median is 71%. These breeding success values may be fitted adequately by a beta distribution ($\alpha=6.55$ and $\beta=2.86$; fitted curve overlain on data in Figure 4.2; goodness-of-fit measured by chi-squared test, $p>0.6$). This beta distribution will be used later for modelling the population dynamics.

4.3 Case Studies

There are sufficient nest observation data for two Cape Vulture colonies (Colleywobbles in the Transkei and Potberg in the southwestern Cape) to warrant a more detailed analysis of breeding performance. The aims of this analysis are first, to estimate the proportion of sexually mature birds which actually attempt to breed, and secondly, to estimate breeding success.

In the southwestern Cape it is possible to get crude estimates of the proportion of adults which have bred because the population is almost totally isolated from the rest of the Cape Vulture population, and complete counts of the local population have been made. As the total number of sexually mature birds in the region has also been counted together with the number of breeding attempts, it is possible to estimate the breeding proportion directly.

At Colleywobbles it is not possible to count the total population, so an indirect method has been developed to estimate the proportion of birds which attempt to breed in any given year. This is based on counts of the number of nest sites which have been 'tenanted'. A nest site is rated as tenanted if an adult Cape Vulture is seen to stand at the nest site for extended periods in the early stages of the breeding season. Other signs of tenanting are the presence of two birds as a pair, copulation or nest building. Because a nest is a valuable resource, adults tend to tenant only one site during a breeding season. Thus the proportion of pairs which tenant a nest site and then go on to lay an egg provide a lower limit on the proportion of adults which breed, and in turn, this yields an upper limit to the proportion of adults which do not breed.

From studies of many different species it is now well established that there are great asymmetries in breeding success, with some small proportion of females providing the great majority of the next generation's breeding females (see Newton 1989 and references therein). It will be shown from the Colleywobbles data that a large proportion of the nestlings are produced from a small proportion of the nests. This has important consequences for modelling the population dynamics because a 10% increase in the number of breeding attempts at a colony will not necessarily lead to a 10% increase in productivity.

4.3.1 Colleywobbles

It has been argued that Colleywobbles is an excellent location for a long-term study of Cape Vulture breeding (Vernon, Piper & Schultz 1982: 109-110):

> Being situated in a region of pastoral people where stock densities are high and animal husbandry techniques primitive, the vultures are mainly free from the factors of modern intensive agriculture which adversely affect them and their breeding. ... Colleywobbles is an ancestral colony that has been in existence since at least the 1890's. It was first reported [to science] by Pringle (1974). ... There is

> little information about the breeding biology of the Cape Vulture in a natural environment of free-ranging game herds on vast grassland plains, and now such information will never be obtained. Thus studies of the vultures at Colleywobbles, in one of the least modified environments, can provide an indication of the potential reproductive capability of the Cape Vulture, and a standard against which to assess their performance at other breeding colonies.

The data collected during the decade of the 1980s (i.e. 1980 to 1989; the 'study-period') have been presented elsewhere (Vernon & Piper 1991) and have been subjected to a number of preliminary analyses (Vernon, Piper & Schultz 1980, 1982, 1983, 1984; Vernon & Piper 1984, 1986, 1988, 1991). In this analysis three questions are to be addressed.

1) At what proportion of tenanted nests is an egg actually laid each year?
2) Of the nests in which an egg has been laid what proportion finally produce a large nestling?
3) How does breeding success vary among breeding attempts?

Before laying an egg (usually during the month of May) adult Cape Vultures will choose a nest site and visit it regularly from some time in March or April. They will tenant the site by standing at it, repulsing other birds that attempt to land at it, they may copulate there and finally they may start to bring nest material to it. Many of those tenanted nests will subsequently be laid in (Figure 4.3) and the proportion actually used are taken to be an upper bound on the proportion of the adult population which breed in any given year (Table 4.8).

Table 4.8
Number of nests tenanted, eggs laid and hatched and large fledglings produced.
(Visible nests only, Main Cliff at Colleywobbles.)
(95% confidence limits estimated from binomial distribution; Diem & Lentner 1970: 85 ff.)

					Estimated Proportion tenanted			Estimated Breeding success		
Year	Tenanted nests	Laid in	Hatchlings	Nestlings	low 95%	%	high 95%	low 95%	%	high 95%
1980	157	125	119	95	72.6	79.6	85.9	68.5	76.0	83.5
1981	160	147	114	107	87.5	91.9	96.1	65.6	72.8	78.0
1982	135	108	87	83	72.5	80.0	86.8	68.9	76.9	84.8
1983	165	112	86	81	59.2	67.9	75.0	64.0	72.3	80.6
1984	159	125	98	92	71.4	78.6	85.0	65.9	73.6	81.3
1985	161	134	100	98	76.9	83.2	89.0	65.6	73.1	80.6
1986	174	157	135	128	85.6	90.2	94.6	75.5	81.5	87.6
1987	164	150	128	104	87.0	91.5	95.7	62.0	69.3	76.7
1988	190	162	137	129	79.8	85.3	90.3	73.4	79.6	85.8
1989	181	167	150	129	88.2	92.3	96.2	70.9	77.3	83.6
Total	1646	1387	1154	1046						

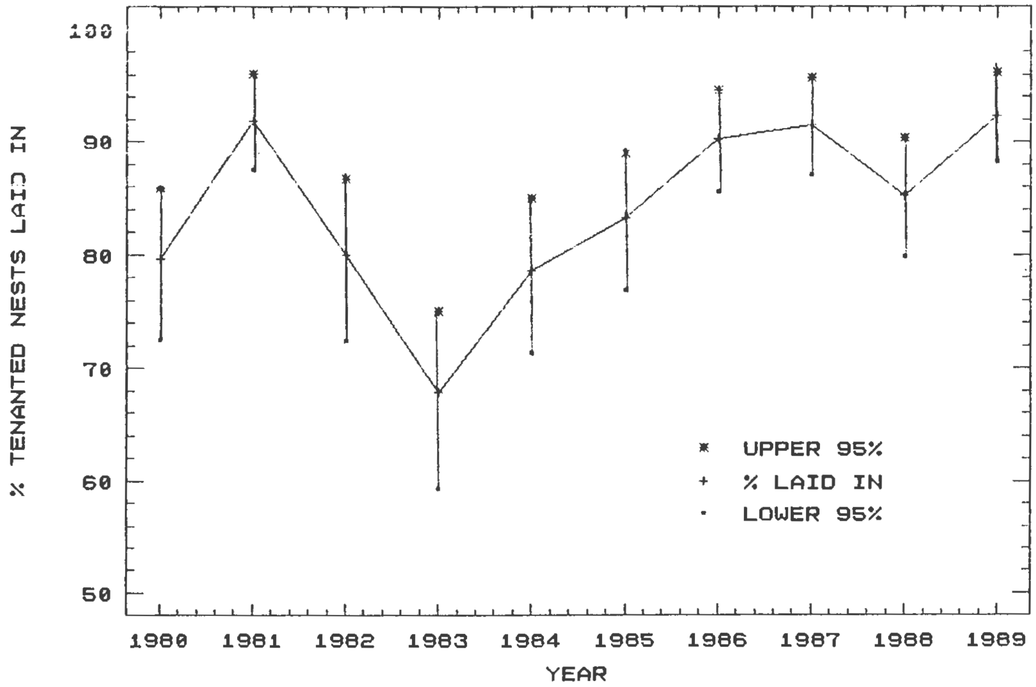


Figure 4.3 Proportion of tenanted nests subsequently laid in plotted against date. (Visible nests only, Main Cliff at Colleywobbles.) (Binomial 95% confidence limits from Diem & Lentner 1970: 85 ff.)

The number of visible nests tenanted on Main Cliff varied from 135 to 190 (Table 4.4), but this does not constitute a significant difference from the average value of 164.6 (Chi-squared = 12.2, 9 d.f., p>0.1). On average 84.3% (95% limits are 83.4 - 85.2%) of tenanted nests were laid in and the proportion did not vary significantly from year to year (Chi-squared = 10.8, 9 d.f., p>0.1).

Table 4.9

Number of nests tenanted, eggs laid and proportion laid in, with chi-squared tests for constancy. (Visible nests only, Main Cliff at Colleywobbles.)

Year	Nests Tenanted	Expected	Chi-squared	Laid in	Ratio	Expected	Chi squared
1980	157	165	.35	125	79.6	132.3	.40
1981	160	165	.13	147	91.9	134.8	1.10
1982	135	165	5.32	108	80.0	113.8	.29
1983	165	165	.00	112	67.9	139.0	5.26
1984	159	165	.19	125	78.6	134.0	.60
1985	161	165	.08	134	83.2	135.7	.02
1986	174	165	.54	157	90.2	146.6	.73
1987	164	165	.00	150	91.5	138.2	1.01
1988	190	165	3.92	162	85.3	160.1	.02
1989	181	165	1.63	167	92.3	152.5	1.37
Total	1646		12.17	1387	84.3		10.81

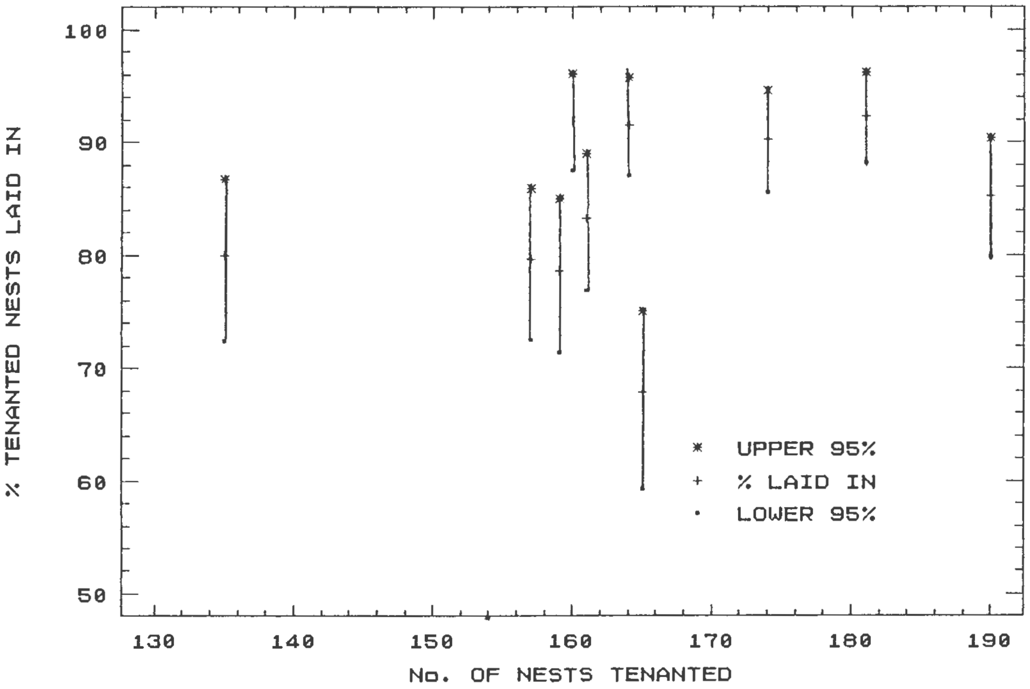


Figure 4.4 Proportion of tenanted nests subsequently laid in plotted against number of tenanted nests. (Visible nests only, Main Cliff at Colleywobbles.) (Binomial 95% confidence limits from Diem & Lentner 1970: 85 ff.)

The proportion of tenanted nests subsequently laid in did not show any significant functional relationship with the number of nests tenanted, i.e. there was no evidence of density dependence in this factor (Figure 4.4).

The 'raw' breeding success may be computed from the ratio of nestlings produced to eggs laid (Table 4.8; Figure 4.5). It is 75.4% with 95% confidence limits of 73.2% to 77.7% (based on a normal approximation). This ratio is given the designation 'raw' because the number of nestlings produced is taken from the last visit made to Colleywobbles each breeding season. In four years the last visit was in October, in five years it was during September, but in one year it was only in early August (Vernon & Piper 1991). As breeding success is taking to be the number of nestlings produced up to 15 September, this implies that the uncorrected counts will in some cases under-estimate, and in other cases over-estimate the breeding success. This effect is modelled and corrected for. The year with the highest 'raw' breeding success is also the only one in which the last visit was during August (Vernon & Piper 1991).

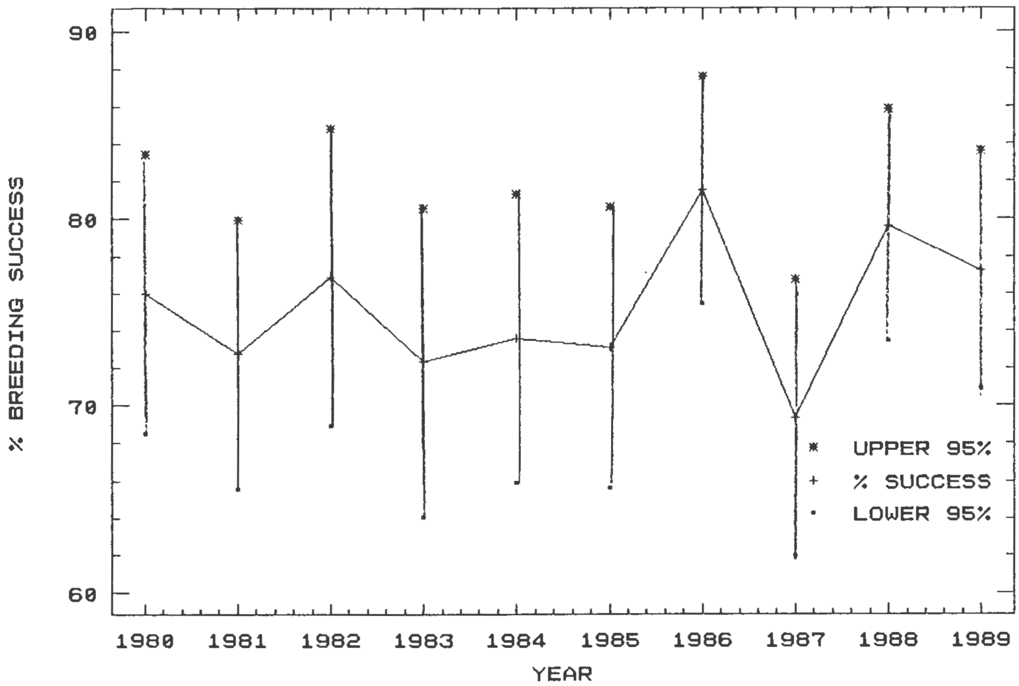


Figure 4.5 Breeding success plotted against year. (Visible nests only, Main Cliff at Colleywobbles.) (Binomial 95% confidence limits from Diem & Lentner 1970: 85 ff.)

The number of eggs laid each year varies from 108 to 167 (mean 138.7). The extent of this variation is greater than can be attributed to random sampling from a constant population (chi-squared = 28.3, 9 d.f., $p<0.01$). However, breeding success does not vary significantly between years (Chi-squared = 15.1, 9 d.f., $0.1<p<0.05$; Table 4.10) and furthermore there is no obvious functional relationship between breeding success and number of eggs laid (Figure 4.6), i.e. there is evidence of no density dependence for this parameter.

Table 4.10
Number of eggs laid and breeding success with chi-squared tests for constancy.
(Visible nests only, Main Cliff at Colleywobbles)

Year	Laid in	Expected	Chi-squared	Nest-lings	Ratio	Expected	Chi-squared
1980	125	139	1.35	95	76.0	105.3	1.01
1981	147	139	.50	107	72.8	123.9	2.30
1982	108	139	6.80	83	76.9	91.0	.70
1983	112	139	5.14	81	72.3	94.4	1.90
1984	125	139	1.35	92	73.6	105.3	1.69
1985	134	139	.16	98	73.1	112.9	1.97
1986	157	139	2.41	128	81.5	132.3	.14
1987	150	139	.92	104	69.3	126.4	3.97
1988	162	139	3.91	129	79.6	136.5	.41
1989	167	139	5.77	129	77.3	140.7	.98
Total	1387		28.32	1046	75.4		15.07

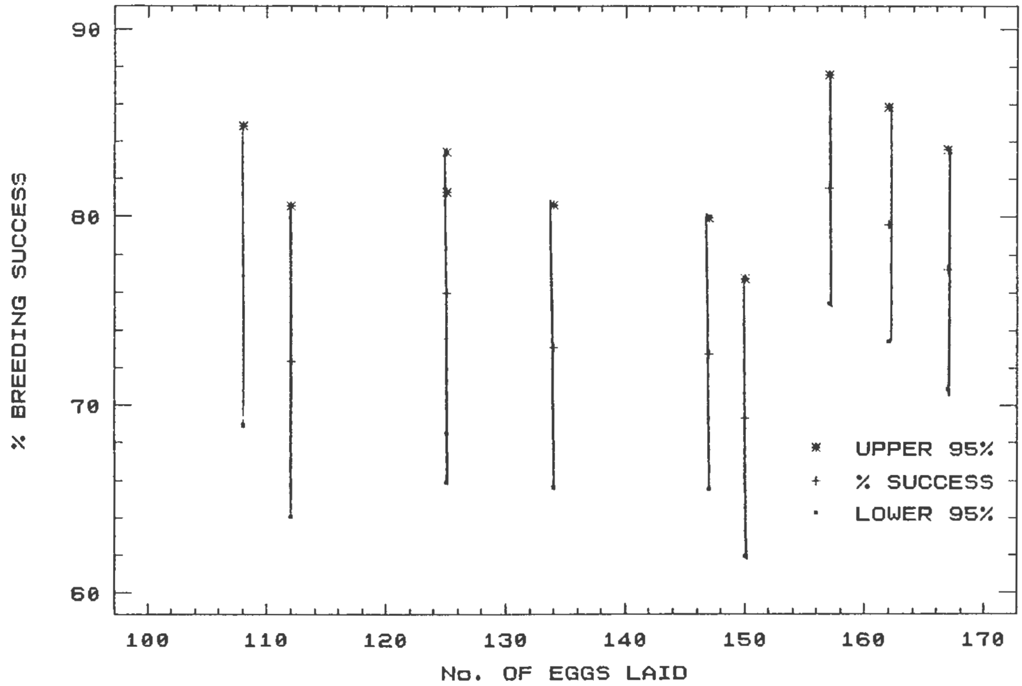


Figure 4.6 'Raw' breeding success for visible nests on Main Cliff as a function of number of nests laid in. (Binomial confidence limits at 95% from Diem & Lentner 1970: 85 ff.)

Each of the 240 visible nests on Main Cliff has been monitored for the entire decade of the 1980s. From these data it is possible to compute the number of nestlings produced from each nest. By counting the number of eggs laid in each nest, it is also possible to estimate the breeding success of those groups of nests in which eggs have been laid ten years out of ten, nine years of ten and so on (Table 4.11). It is readily apparent that the breeding success is higher for nests used most often (Figure 4.7). By transforming breeding success, using a logit transform, and regressing against the number of breeding attempts, it is seen that less used nests have a significantly lower breeding success (motivation for the use of a generalized linear model for a binomial response variable may be found in Chapter Three). This is model is constructed in the following manner.

Define: $p(n)$ = Probability that a nest will successfully produce a large fledgling given that it was laid in exactly n times in the decade 1980 -1989.

$\text{Logit}\{p(n)\} = \text{Ln}\{p(n)/[1-p(n)]\}$

The linear model is:

$\text{Logit}\{p(n)\} = a + b*n$

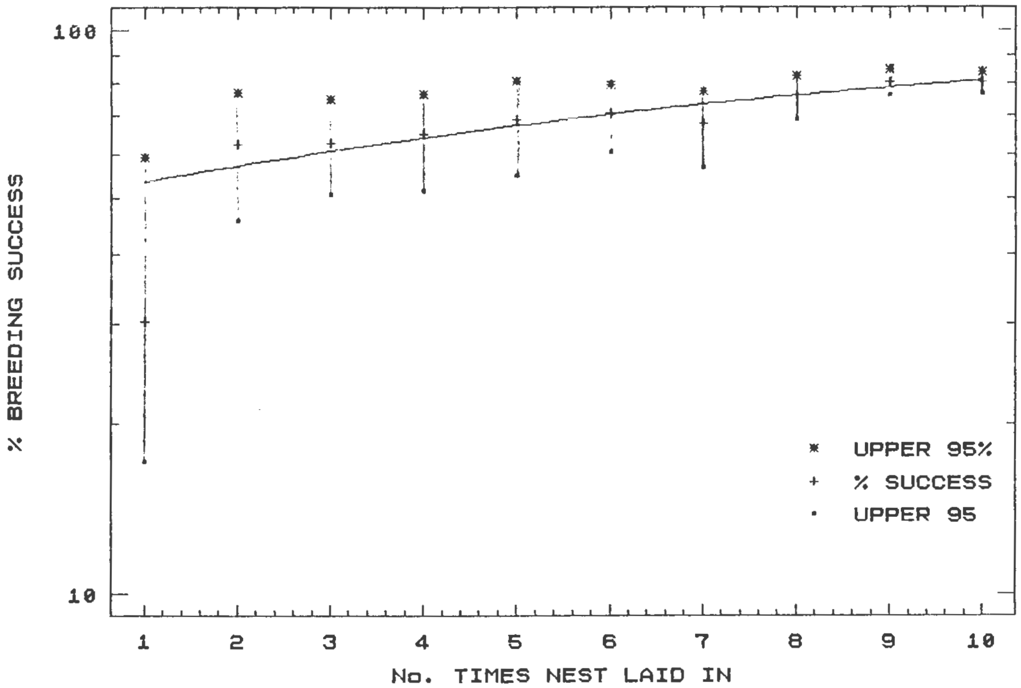


Figure 4.7 Breeding success for visible nests on Main Cliff as a function of number of times nest laid in. (Binomial 95% confidence limits from Diem & Lentner 1970: 85 ff.)

The fitted model is (standard error of the estimate in parentheses):

$$\text{Logit}\{p(n)\} = 0.14570\,(\pm 0.00795)*n$$

The regression goes through the origin, i.e. the constant was not different from zero ($p>0.05$). The inverse model is:

$$p(n) = \exp(a+b*n)/\{1+\exp(a+b*n)\} = \exp(0.14570*n)/\{1+\exp(0.14570*n)\}$$

This predictor is shown as an overlay on the breeding success graph (Figure 4.7) and it can be seen that the fit is excellent.

From a consideration of which nests are used in any given year, it is clear that those nests used every year will always be used in any given year. Those nests used in nine of the ten years have a high chance of being used in any given year. By examining the nests used each year it follows that nests used less frequently are only used in those years in which the number of nests laid in is high (Figure 4.8). Because the least frequently used nests are also the least successful nests it is to be expected that the years with the highest number of eggs laid should also be the years with the lowest average breeding success. In other words, this simple model predicts that there should be some form of density dependence. But, this is not so (see Figure 4.6). Why? A more sophisticated model is called for.

Table 4.11
Frequency of nest use on Main Cliff and the number of nestlings reared: 1980-1989.

Number of nestlings reared	Number of times nest used (= 'laid in') 1	2	3	4	5	6	7	8	9	10	Total
0	14	4									18
1	8	7	8	4							27
2		9	8	3	3	3					26
3			6	3	2	1	2				14
4				5	4	3	4	2	2		20
5					2	7	3	4	1	2	19
6						2	1	6	6	1	16
7							2	6	8	14	30
8								2	15	14	31
9									4	10	14
10										7	7
Total	22	20	22	15	11	16	12	20	36	48	222
Nestlings	8	25	42	39	38	68	57	122	261	386	1046
Potential	22	40	66	60	55	96	84	160	324	480	1387
% Success	36	63	64	65	69	71	68	76	81	80	75
% Potent.	4	13	19	26	35	43	48	61	73	80	47
% Sites	10	9	10	7	6	7	5	9	16	22	100
% Nestlings	1	2	4	4	4	7	5	12	25	37	

Each of the 1231 nest-years in which an egg was laid, and for which a laying date had been estimated were subject to a GLM (generalized linear model) analysis. The variables used in the model were as follows.

1) Date of last visit relative to 15 September (+^{ve} being later and -^{ve} earlier). It was suggested above that those nests last counted early in the season would have their nest losses underestimated. So this variable is included to model that effect.
2) Laying date. (Coded as five dummy 0/1 variables: laid in April, 1-10 May, 11-20 May, 21-30 May and June.) It is suspected that pairs which lay early in the season do so because they are fitter and thus it is likely that they will be more successful in bringing forth large nestlings.
3) Year. (Coded as nine dummy 0/1 variables, one for each year 1981 to 1989; 1980 is treated as the base year.)
4) Number of breeding attempts in the ten year study period.
5) Density, i.e. number of eggs laid in a given year. (It should be noted that density-dependent effects could act earlier in the breeding cycle, e.g. at pairing or nest building; A. Dhondt, pers. comm.)

As the dependent, or response variable was a binary (i.e. 0/1), or binomial variable, a logit transform was used (though one is not constrained to canonical transforms; BTJ Morgan, pers. comm.). Variable selection was by forward selection and backward elimination leading to a parsimonious model which was compatible with the data. In this final model the logit transform of breeding success is related to the following variables (the value in parenthesis is the standard error corresponding to the associated parameter estimate):

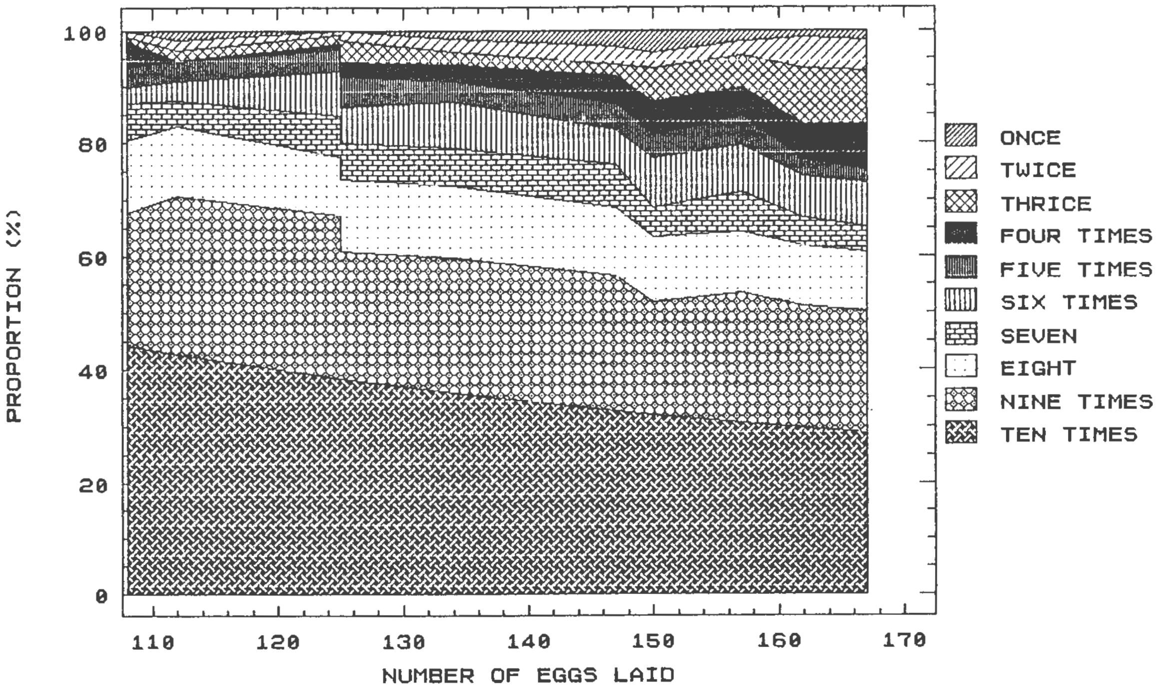


Figure 4.8 Frequency of nests use. The nests only laid in once, twice or thrice tend to be utilized in the 'good' years, i.e. the years in which many eggs are laid.

Logit (Breeding success) = -0.00526 (±0.00361) per day from 15 September
+0.1238 (±0.0105) per additional breeding attempt
+1.273 (±0.454) if laid in April
+1.168 (±0.274) if laid in the period 1 - 10 May
-0.544 (±0.175) if laid in June
+0.645 (±0.231) if the year is 1988
+0.654 (±0.222) if the year is 1989

The goodness of fit of the regression as a whole is satisfactory (chi-squared = 1269, 1224 d.f., $p=0.819$), i.e. the observed values and predicted values do not differ significantly. The coefficients of the terms in the regression are all significant ($p<0.01$), except for date of last visit ($0.2<p<0.1$). The date of last visit is included (even though it is not significant) to correct for the unobserved nest losses.

The following interpretation of the model is offered.

1) The logit decreases by 0.00526 for each day the colony is visited (i.e. subjected to census) after 15 September.

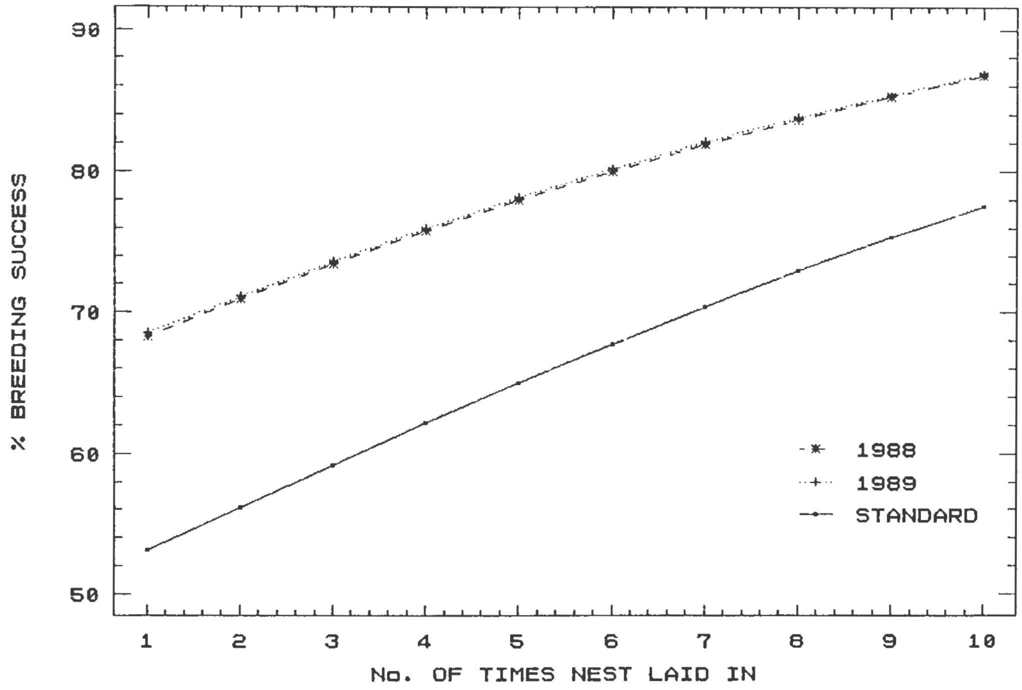


Figure 4.9 Behaviour of the Logistic model for breeding success: The effect of year. It should be noted that the two curves for 1988 and 1989 are almost indistinguishable.

2) For a nest laid in three times during the decade the logit will be higher by 0.1238 than one laid in twice; i.e. each additional time the nest is laid in during the decade the logit increases by 0.1238.
3) Early nests are more successful by 1.273 if laid in during April and by 1.168 if laid in during 1-10 May, but less successful by -0.544 if laid in during June.
4) The years 1988 and 1989 were more successful by differentials of 0.645 and 0.654, respectively.

To investigate the nature of the logistic relationship a number of 'special cases' are considered.

1) Standard Nest. Let the standard nest be one last inspected on 15 September, laid in five times during the decade with the egg laid in the last two-thirds of May in a year before 1988. The predicted breeding success is = 0.65
2) Standard nest, but laid in during 1988. Success = 0.7797
3) Standard nest, but laid in during 1989. Success = 0.7813. The way in which breeding success varies for nests laid in during 1988 or 1989, and with varying number of times laid in, shows a monotonic increase (Figure 4.9).

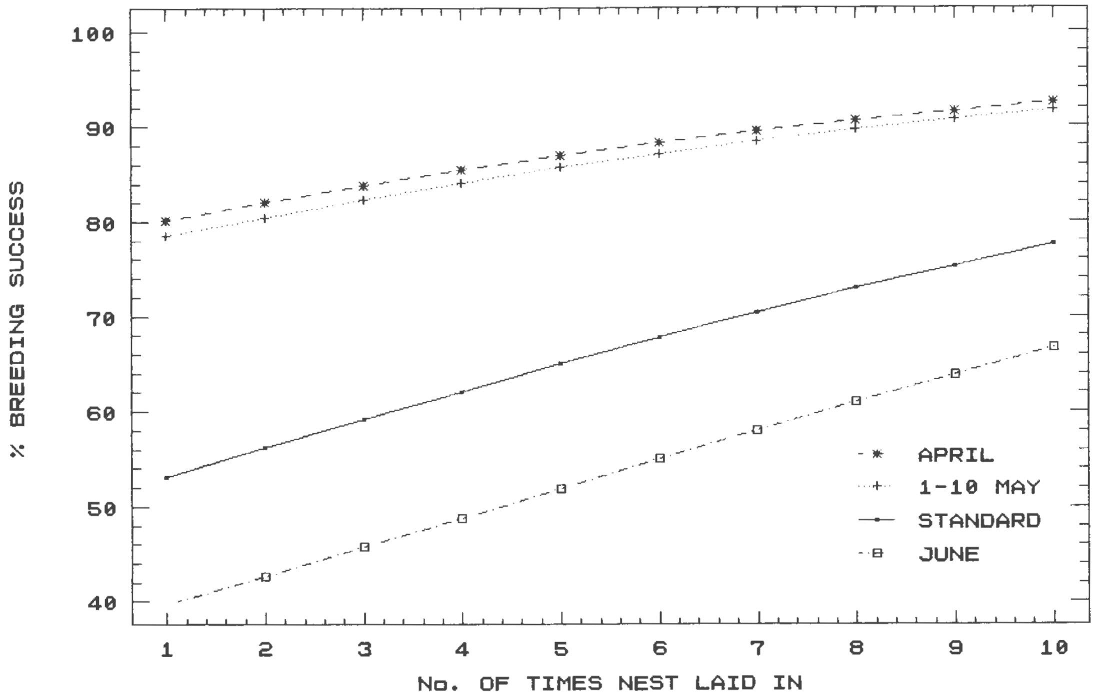


Figure 4.10 Behaviour of the Logistic model for breeding success: The effect of date of laying.

4) Standard nest, but laid in during April, 1-10 May or June will have a predicted breeding success of 0.8690, 0.8566, or 0.5187, respectively. The response will also vary in a monotonic fashion (Figure 4.10).
5) As the date of last visit is extended beyond 15 September the breeding success will decrease (Figure 4.11).

In summary, the model suggests that breeding success is primarily a function of the following effects.

1) Date egg laid, with early nests having a much greater chance of success than later nests. This is the most important effect.
2) Number of times nest used. The nests used most often are the most successful (or the other way around, see page 197 for discussion).
3) Year. Some years are better than other years, but there is no evidence of density dependent effects for breeding. In fact, there seems to be a tendency for years with the highest number of eggs laid to be the most successful. This may be related to some form of food trigger in the environment, i.e. those years with a trigger for more breeding attempts may also be the years with the highest overall food supply, and so will produce the highest breeding success.

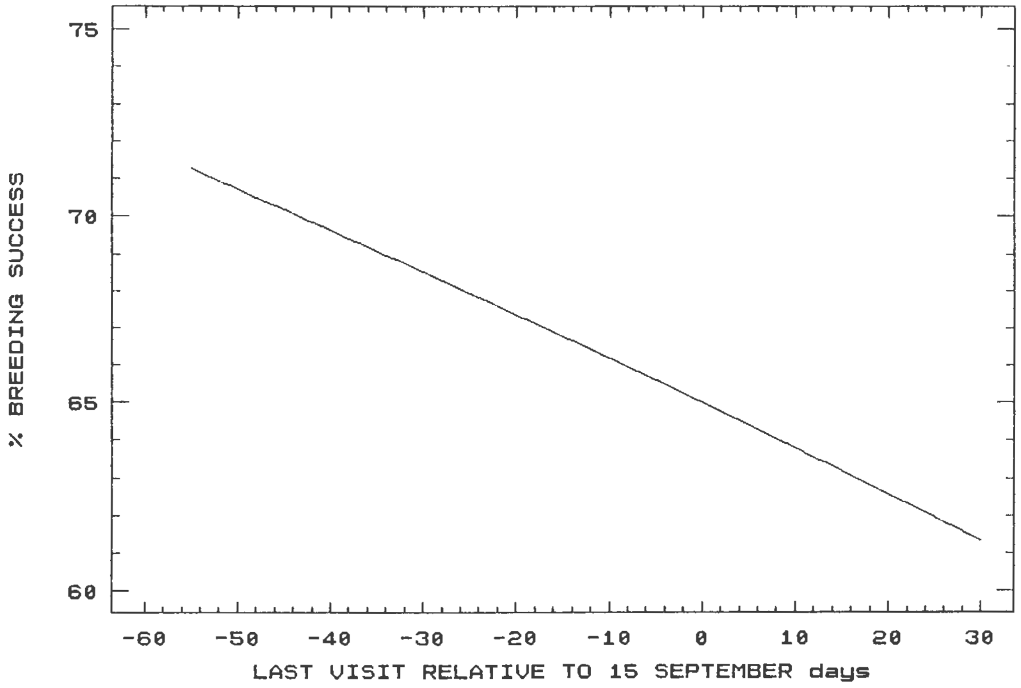


Figure 4.11 Behaviour of the Logistic model for breeding success: The effect of date of late census.

4.3.2 Colonies in the southwestern Cape

Over the last forty years, several observers have monitored the Cape Vulture breeding colony at Potberg, near Bredasdorp, in the southwestern Cape. During the 1980s, breeding was also noted at a number of sites further inland and from observations of colour ringed birds it may be concluded that there is a considerable interchange between these sites (see Chapter Six for a detailed analysis of movements).

There are 16 years of breeding success estimates for Potberg, seven years for Aasvogelvlei and one year each for Boschbeg, Perdeberg and Platterug (Table 4.12). From 354 eggs laid an estimated 228 nestlings were produced which is a breeding success of 64.4% (approximate 95% confidence limits from normal approximation: 59.4% to 69.4%). There were no statistically significant year-to-year, or colony-to-colony variations (Chi-squared = 6.24, 25 d.f., $p > 0.1$; Table 4.12).

Table 4.12
Breeding success at five Cape Vulture sites in the southwestern Cape
(Expected number of nestlings computed from 0.6441*Eggs laid).

Site	Colony	Year	Eggs	Nestlings	Brd. Succ.	Expect. Nstlings	Chi-squared	Reference
8	Aasvogelvlei	1981	10	7	70.0	6.44	.0447	Boshoff (1987: 40)
8	Aasvogelvlei	1982	8	5	62.5	5.15	.0047	Ditto
8	Aasvogelvlei	1983	11	5	45.5	7.09	.8692	A.F. Boshoff (*in litt.* 22-01-85 to S.E. Piper)
8	Aasvogelvlei	1984	8	4	50.0	5.15	.3321	Ditto
8	Aasvogelvlei	1985	9	6	66.7	5.80	.0069	Boshoff (1987: 40)
8	Aasvogelvlei	1986	10	8	80.0	6.44	.3039	Ditto
8	Aasvogelvlei	1987	9	7	77.8	5.80	.2069	A.F. Boshoff (pers. comm.); Boshoff & Scott (1990: 34)
239	Boschberg	1990	2	1	50.0	1.29	.0830	Boshoff & Scott (1990: 34)
69	Perdeberg	1988	2	2	100.0	1.29	.2534	Ditto
-	Platterug	1988	10	9	90.0	6.44	.7278	Ditto
68	Potberg	1975	37	23	62.2	23.83	.0300	Boshoff (1981: 7)
68	Potberg	1976	24	16	66.7	15.46	.0184	Ditto
68	Potberg	1977	22	15	68.2	14.17	.0460	Ditto
68	Potberg	1978	15	9	60.0	9.66	.0485	Ditto
68	Potberg	1979	17	10	58.8	10.95	.0901	Boshoff & Vernon (1981); Boshoff (1981)
68	Potberg	1980	14	8	57.1	9.02	.1293	Boshoff (1981: 7)
68	Potberg	1981	16	10	62.5	10.31	.0093	Boshoff (1987)
68	Potberg	1982	17	14	82.4	10.95	.6648	Ditto
68	Potberg	1983	14	7	50.0	9.02	.5812	Ditto
68	Potberg	1984	17	9	52.9	10.95	.4221	Ditto
68	Potberg	1985	13	6	46.2	8.37	.9384	Ditto
68	Potberg	1986	11	7	63.6	7.09	.0010	Ditto
68	Potberg	1987	12	8	66.7	7.73	.0092	Boshoff & Scott (1990: 34)
68	Potberg	1988	13	8	61.5	8.37	.0174	Ditto
68	Potberg	1989	14	11	78.6	9.02	.3575	Ditto
68	Potberg	1990	19	13	68.4	12.24	.0447	Ditto
			354	**228**	**64.41**		**6.2405**	

However, the breeding success was exactly eleven percentage points lower in the southwestern Cape than at Colleywobbles (i.e. 64.4% vs 75.4%; Table 4.13; chi-squared = 17.4, 1 d.f. $p<0.001$). These data are, in the main, from comparable periods during the 1980s so that the differences are likely to be real and not the result of temporal trends. The colony at Colleywobbles is in 'prime' habitat (see section 4.3.1 above), while the southwestern Cape is a winter rainfall region and this means that breeding takes place during the wet-season of wind, mist and rain (Robertson 1986). Furthermore, there is much use of poison by local livestock farmers on sheep (for control of flies and the like) farmed around the colony. It is likely these substances are regularly picked up by the Cape Vultures which forage on the carcasses.

Table 4.13

Breeding success at Colleywobbles compared with that at the five Cape Vulture sites in the southwestern Cape.

	Eggs		Nestlings	
Region	Laid	Lost	Reared	Breeding Success
Colleywobbles	1387	341	1046	75.41%
S.W. Cape	354	126	228	64.41%
Total	1744	467	1274	73.05%

4.4 Summary

From an enumeration of all known sites used by Cape Vultures, it is known that about 83 of these are used as breeding colonies. The total number of breeding pairs is estimated at 4400, but no confidence limits are available for this number. These breeding birds occur in two major concentrations, the main one being in the Transvaal and Botswana and the lesser one being in Transkei, Lesotho and the Natal Drakensberg. In addition, there are two small and isolated populations, one in Namibia and the other in the southwestern Cape.

Only 33 of the 83 breeding colonies (i.e. 43%) have been assessed as to trends in the numbers of breeding pairs. Of these 33 colonies 11 (33%) are decreasing, 16 are stable (48%) and six are increasing (18%). Of the six increasing colonies, five have been enumerated using helicopter-based photographic methods and it is probable that part of the ‘increase’ in the numbers of nests counted can be ascribed to improved census technique (Benson, Allan, Tarboton & Dobbs 1990).

By analogy with species of similar lifestyle and body size, and from limited direct observation it is suggested that the average age of first breeding is likely to be somewhere in the range 5-7 years.

The proportion of adults which breed in any one year is estimated from a number of observations, and by analogy with other species, and is likely to be between 70% and 90%. At Colleywobbles, the proportion of tenanted nests in which an eggs was laid (i.e. taken as an upper bound on the proportion breeding) varied from 67.9% to 92.3% over ten years and had a mean value of 84.3% (95% confidence limits: 83.4% to 85.2%). While it is likely that the proportion of adults which breed varies with age, there are no data available for estimating the magnitude of this effect in the Cape Vulture, nor for any of the other four griffons.

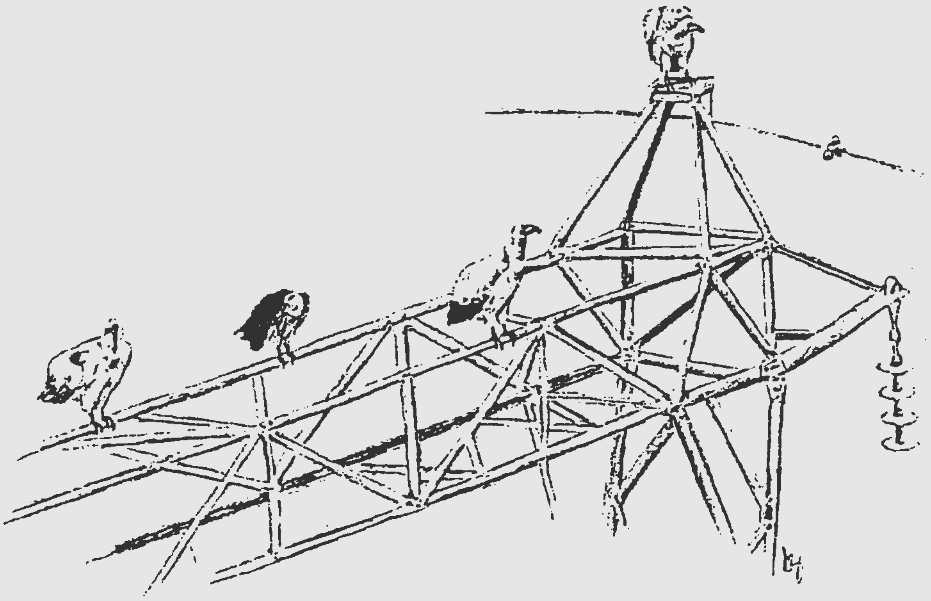
From a comparison of similar species, it is to be expected that breeding success (or productivity, measured as large fledglings per breeding pair p.a.) should be in the range 50% to 80%. An analysis of 29 sets of observations on the Cape Vulture (but ignoring Colleywobbles and the southwestern Cape) reveals that breeding success is likely to average about 70% with lower and upper limits of about 45% and 85%, respectively. Over a ten year period at Colleywobbles, breeding success varied from 69.3% to 81.5% with a mean of 75.4% (95% confidence limits of 73.2% to 77.7%). However, in the southwestern Cape, breeding success was found to be much lower at 64.4% and this is hypothesized to be a function of the Mediterranean-type climate which brings rain during winter (i.e. the breeding season) and the considerable use of chemicals by farmers on sheep (the predominant food source in the region).

A model was built of the losses from egg-laying through to large nestling. It was found that breeding success varied with the following three factors.

1) Date egg laid. Early nests (i.e. late April and early May) were more successful than other nests while late nests (i.e. June) were less successful. It is suggested that high-quality pairs come into breeding condition sooner, are able to lay earlier and are more capable of caring for their egg and subsequent nestling.
2) Nests laid in more often are more successful. It has been suggested (E. Danchin, pers. comm.) that nests are more likely to be deserted after a breeding attempt has failed. Thus pairs which are less successful are more likely to abandon a nest and to try another nest, if they attempt to breed again. An inspection of the relationship between breeding success and the number of times a nest was used (Figure 4.7) indicates that there is a clear increase in breeding success with the number of times a nest was used, from two through to ten breeding attempts. However, for nests used once only the breeding success is much lower than expected. This could be due to low sample size (22 nests out of 222) or it could be an indication of a different process, e.g. these could be pairs 'experimenting' for the first time.
3) Breeding success during the two calendar years 1988 and 1989 was significantly higher than during other years. No environmental reason was found for this.

No density-dependent relationship was found between breeding success and number of breeding attempts. This is not to say the density-dependent effects do not act on breeding; they may act before the egg-laying period, e.g. on the number of birds which form pairs, the number of pairs which attempt to come into breeding condition, the proportion which attempt to secure a nest site and the proportion which build a nest (A. Dhondt, pers. comm.).

No consideration has been given to the physical characteristics of nest sites. Thus it is not known if the more successful nests have bigger ledges, more protection from the elements, etc. Nor is it known if successful nests are clumped together. These factors could account for some of the variability in breeding success (D.C. Houston, pers. comm.).



Chapter Five

Survival

Contents

Abstract

It is not yet possible to provide accurate and direct estimates of survival in adult Cape Vultures. From an examination of the literature (i.e. scavengers of similar size and lifestyle) it is thought that a reasonable survival rate for adult Cape Vultures is about 90% with an upper limit of not more than 95%. From an analysis of ring-resighting and ring-recovery data it is shown that first year survival is likely to be in the range 45% to 50% p.a. This is a significant improvement on previous estimates. From an investigation of the ring-recovery process it is concluded that there have been significant changes in the way Cape Vultures are reported - over the period 1948 to 1988. The resighting of colour-ringed birds in the south-western Cape is providing estimates of survival in sub-adults which are much better than those from ring-recoveries. They are so much better than those from ring-recovery data that ring-resighting should become the standard approach in the study of survival in this species. A consideration of the causes of death leads to the conclusion that many 'unnatural' mortality factors act against the Cape Vulture and it is necessary to find ways of monitoring the effects of each of these.

Chapter Five

Survival

In the previous chapter on fecundity, various estimates were provided for the number of large fledglings likely to be in the nest at the end of the breeding season. In this chapter it is necessary to consider three questions.

1) How many of those large nestlings make the transition to free-flying fledglings and then independent first-year birds?
2) How many of these first-years reach adulthood, or more strictly speaking an age at which they are capable of being recruited into the breeding population?
3) Once part of the breeding population, what proportion survive from one year to the next?

Naturally it would be an additional bonus if these three questions could be answered as a function of space, time and population density.

In a stable population, over time, there are as many deaths as there are births so that it might seem that it should be possible to estimate the death rate with the same precision as the birth rate. This is just not so, however, because while birth is a slow and easily observed process clumped in space and time, death is instantaneous and often widespread in space and time. How is the rate of death, or its counterpart survival, to be measured?

In technologically advanced human societies where every individual's unique Lexis diagram (Figure 5.1) may be traced, it is possible to monitor survival in a fairly exact way (Lexis 1875: 302 quoted in Keyfitz 1968: 9). If, because of privacy-of-information constraints, only the summary statistics of mortality are available, then it is possible to construct a variety of life-table models to estimate survival (Keyfitz 1968: 12 ff.). If, in addition, regular fine-grid census data are collected for the whole population, then even more sophisticated models may be constructed.

What approaches are available when the individuals are not recognizable and only a small proportion of the deaths are observable? The traditional approach is to place, on a sample of young birds, a unique and individual-specific mark such as a ring (or tag) or set of colour-rings (see review in Clobert & Lebreton 1991: 81 ff.). Two broad approaches are then employed to estimate the vital statistics. By directly observing marked individuals, data may be collected on their survival, while observing the deaths of marked individuals provides information on mortality. Both these approaches will be used here. Currently these two separate approaches are being brought together and methods for providing survival estimates based on combined recapture (or resightings) data and recovery data are being developed (see review by Buckland & Baillie 1987).

In addition to deriving estimates for survival as a function of various parameters (e.g. age and space) it is important to consider how various unnatural mortality factors impinge on the Cape Vulture. It is necessary to estimate the mortality effects that these factors have as well as to attempt to determine if their effects are additive or merely replace existing and natural mortality factors, i.e. are they compensatory?

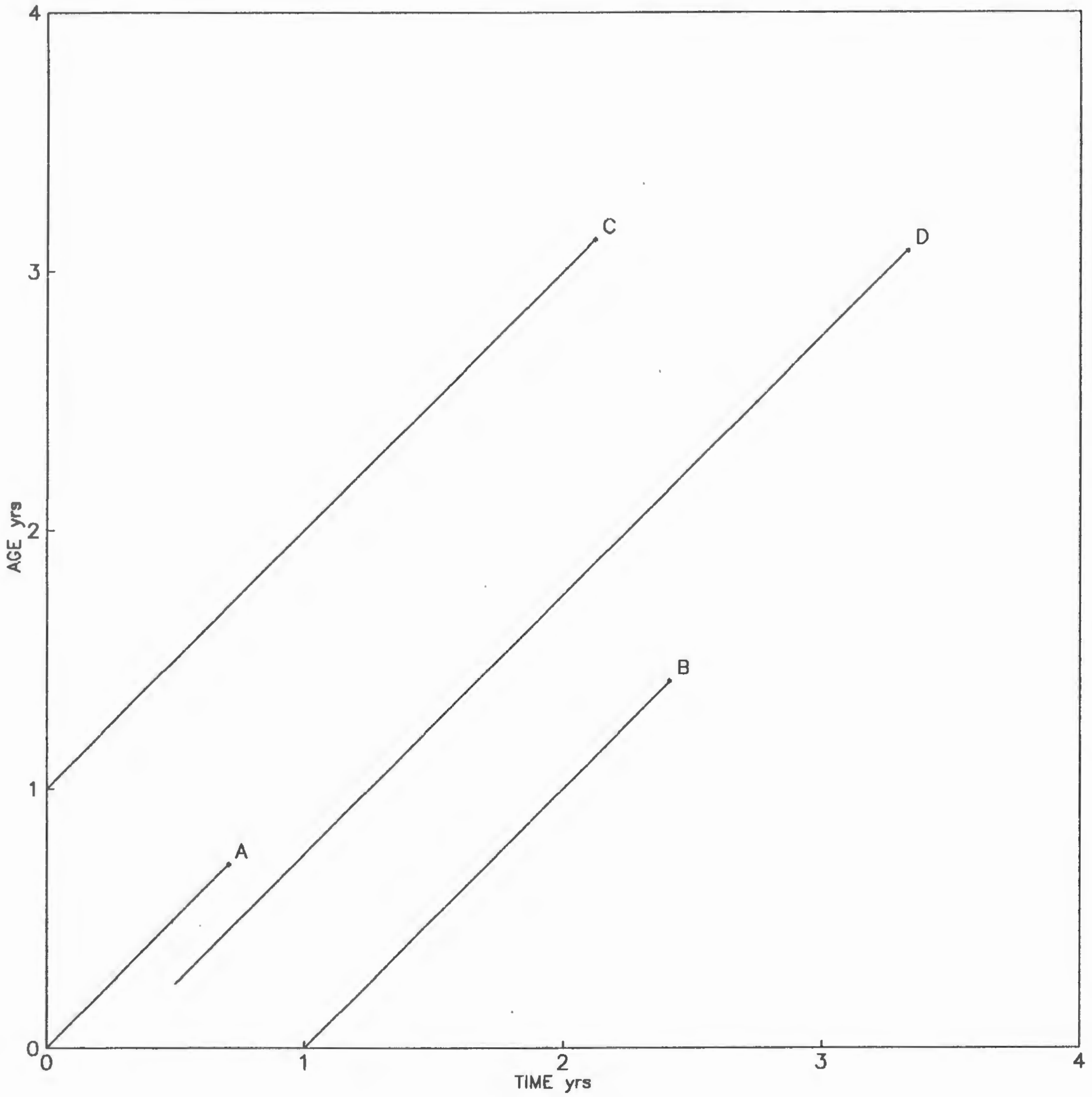


Figure 5.1 Lexis diagram. Individual A was hatched at time zero when it was ringed. It lived for less than a year. Individual B was hatched at time 1 and ringed then, living for one an a half years. Individuals C and D were ringed some time after they were hatched, but at known ages.

5.1 Estimates of survival and longevity: an interspecific comparison

There are few reliable estimates of survival and longevity for the Cape Vulture. One way to make good this deficit is to draw comparisons with other species of similar size and life-history. It is from these comparisons that reasonable limits will be set on estimates of adult survival in the Cape Vulture. In addition, crude estimates will be provided for other survival parameters (e.g. first year survival and proportion of fledglings recruited to the adult population).

Estimates of survival: an interspecific comparison

The late Leslie Brown long advocated the use of an indirect method for estimating adult survival among birds from population structure. This technique is based on the often implicit assumptions that the population size is constant, the age structure stable, the ages of first breeding and acquisition of final plumage equal and known, and the population productivity correctly estimated. This approach has been used to derive three regression equations for adult mortality as a function of body mass (Brown & Pomeroy 1984: 102, 110). Each equation is based on a slightly different set of assumptions or data (mortality is measured as % p.a. and the mass in grams).

$$\mathrm{Log}_{10}(\mathrm{Mortality}) = 1.88 - 0.19 * \mathrm{Log}_{10}(\mathrm{Mass})$$
$$\mathrm{Log}_{10}(\mathrm{Mortality}) = 1.93 - 0.22 * \mathrm{Log}_{10}(\mathrm{Mass})$$
$$\mathrm{Log}_{10}(\mathrm{Mortality}) = 2.18 - 0.42 * \mathrm{Log}_{10}(\mathrm{Mass})$$

The estimated mortality rate for adult Cape Vultures is 11.6%, 13.6% and 3.4% from each of these three formulae, respectively (equivalent survival rates are 88.4%, 86.4% and 96.6%). These estimates must be treated with some caution, for two reasons. First, the population structure data come from less than random samples (loc. cit.; Piper, Mundy & Ledger 1981) and secondly, the equations were fitted to raw percentages which is statistically undesirable (McCullagh & Nelder 1989: 105 ff.) - the authors acknowledge this.[1]

A compilation of adult survival rate estimates has been made from a variety of sources (Table 5.1). Consequent upon my reservations concerning the age-structure method advocated by Brown (1977), little confidence is placed on some of the survival estimates from Brown & Pomeroy (1984). From an examination of these data it is suggested that the Cape Vulture could have an adult survival rate somewhere in the range 90% to 95% p.a.[2]

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[1] One of the examiners (E. Danchin) said "I do not agree with the method which links any life history parameter to adult body mass". I am not unhappy with this sentiment; all I am trying to do here is get a feel for what could be a *reasonable* value for adult survival.

[2] It has been shown for the Eurasian Griffon that it is possible for the adult survival rate to be as high as 99% p.a., F. Sarrazin, pers. comm. (see Piper 1982). This high survival was noted for a small population which is tightly managed as part of a vulture re-introduction programme.

Table 5.1

Estimates of adult survival (as percent per annum) in some large scavengers.

Species	Survival % p.a.	Method	Mass g	Source and comments
Marabou	92	?	?	Pomeroy (1977a)
Bateleur	88.4	Ageing	2250	Brown & Cade (1972)
	97	Ageing		Brown & Pomeroy (1984: 101)
Bearded Vulture	98	Ageing	5760	Brown & Pomeroy (1984: 101)
	95	Ageing	5740	Brown (1988: 475-476)
Fish Eagle	97	Ageing	2500	Brown & Pomeroy (1984: 102)
Palmnut Vulture	95	Ageing	1500	Brown & Pomeroy (1984: 104)
Herring Gull	91.7	Resighting	900	Coulson & Butterfield (1986)
Turkey Vulture	78.5	?	?	Stewart (1977)
Black Vulture	60	?	?	Stewart (1983)
Andean Condor	94	Resighting	?	Temple & Wallace (1989)
Albatrosses				
Wandering	90	Resighting	9000	Rothery & Prince (1990)
Greyheaded	95	Resighting	3800	Ditto

From a mathematical model of the population dynamics of the California Condor it has been estimated that the adult survival rate must be at least 95% for the population not to decline (Verner 1978). Using a slightly different model a 'reasonable estimate' of 94% has been suggested for the same parameter (Mertz 1971). This New World vulture is similar in life-history to the Cape Vulture, but slightly larger, and thus likely to be more K-selected. Thus an upper limit of 95% p.a. seems to be a reasonable assumption for survival in adult Cape Vultures.

Estimates of Survival in the Cape Vulture

The earliest estimates of survival in the Cape Vulture (all age-classes combined) were made using ring recoveries (Houston 1974). Estimates of annual survival were 45 ±16% assuming the ring recoveries complete and 56 ±5.6% assuming they were incomplete, using the method of Haldane (1955). However, Houston (1974) added 'The figure of approximately 50% annual mortality ... for the Cape Vulture cannot be considered valid'.

This was followed by a second analysis of the ring-recovery data-set after it had been purged of errors and a considerable number of new recoveries had been added (Ledger & Mundy 1978; Piper, Mundy & Ledger 1981). Survival estimates were provided on an age-specific basis for the first, second, and third and subsequent years. Considerable reservation was expressed because the ringing-recovery process is complex and not easily modelled (Piper, Mundy & Ledger 1981). These reservations were later confirmed in criticisms of the analysis (Anderson, Burnham & White 1985, Clobert & Lebreton 1991: 82, K.H. Lakhani, pers. comm.).

First year survival.

At Potberg during the two breeding seasons of 1981 and 1982 a total of 21 nestlings was ringed and either four or six of them survived to the end of their first year (Robertson 1984). Four out of 21 gives $S_1 = 19.0\%$ (95% limits: 5.5% to 41.9%) but six out of 21 gives $S_1 = 28.6\%$ (95% limits: 11.3% to 52.2%). The equivalent estimate from Piper, Mundy & Ledger (1981) is 17% (95% limits: 14% to 49%). Thus these two estimates are of similar magnitude.

Adult survival.

Of seven recognizable (i.e. fitted with colour rings) adult Cape Vultures breeding at the start of the 1981 breeding season at Potberg five were there the next year (Robertson 1984). Five out of seven gives $S_a = 71.4\%$ (95% limits: 29.0% to 96.3%). The equivalent estimate from Piper, Mundy & Ledger (1981) is 74% (95% limits: 56% to 92%). Again, these limits are equivalent.

Recruitment to the adult population.

During the three years 1974 to 1976 a total of 48 birds was colour ringed at Potberg and four of these were seen to breed there in the year 1981, or later (Robertson 1984); recruitment rate, $P_r = 8.3\%$ (95% limits: 2.3% to 19.9%). The equivalent figure from Piper, Mundy & Ledger (1981) is 7.7%, which is similar.

Estimates of longevity: an interspecific comparison

There is an intrinsic interest in longevity, stemming from an attitude epitomized in the 'Guinness Book of Records'. In conversations with keepers of caged birds there are two measures they use to quantify the quality of their operations: breeding success and longevity (pers. obs.). Thus in the zoo-orientated literature there are a number of records of longevity. These are summarized (Table 5.2), and a number of conclusions may be drawn from them.

It has been known for some time that many life-history parameters 'scale' with animal size, i.e. larger animals have higher survival, lower fecundity and live longer than small animals. For raptors, the predictive equations for longevity, T (in years) as a function of mass, M (in grams) are provided Lindstedt & Calder (1976).

$T = 28.3\ M^{0.19}$ for captive birds

$T = 16.6\ M^{0.18}$ for wild non-passerines

Table 5.2
Estimates of longevity (in years) for some large scavengers.
(Some were already adult when taken into captivity, some were still alive when last aged)

Species	Longevity	Captive	Mass	Source and comments
Bateleur	55	Yes	2250	Flower (1923)
Bearded Vulture	26	Yes	5760	Newton (1979)
Cinereous Vulture	30	Yes	9000	Male - Flower (1938: 208)
	32	Yes		Female - Flower (1938: 209)
	39	Yes		Female - Flower (1938: 209)
	32	Yes		Gurney (1899)
	26	Yes		Minnemann & Busse (1984)
	25	Yes		Newton (1979)
	36	Yes		Diebold (1992)
	34	Yes		Ditto
Pondicherry Vulture	23	Yes	?	Minnemann & Busse (1984)
Eurasian Griffon	35	Yes	8500	Flower (1938: 209)
	31	Yes		Two - Flower (1938: 209)
	34	Yes		Female - Flower (1938: 209)
	34	Yes		Gurney (1899)
	35	Yes		Flower (1938: 209)
	31	Yes		Lucas (1970)
	37	Yes		Newton (1979)
Cape Vulture	23	Yes	8500	Flower (1938: 210)
	29	Yes		Flower (1938: 210)
	30	Yes		Flower (1938: 210)
Himalayan Griffon	24	Yes	?	Minnemann & Busse (1984)
Lappetfaced Vulture	24	Yes	6600	Gurney (1899)
	25	Yes		Newton (1979)
	32	Yes		Mendelssohn & Marder (1989)
African Whitebacked Vulture	19	Yes	5400	Flower (1938: 210)
Indian Whitebacked Vulture	17	Yes	?	Flower (1938: 210)
	23	Yes		Minnemann & Busse (1984)
Hooded Vulture	16	Yes	2100	Flower (1938: 210)
Egyptian Vulture	20	Yes	2000	Minnemann & Busse (1984)
	23	Yes		Newton (1979)
Andean Condor	52	Yes	1100	Gurney (1899)
	72	Yess		Moore *et al.* (1985)
California Condor	45	Yes	?	Koford (1953: 22)
	58	Yes		McGahan (1962)
Turkey Vulture	16	?	?	Stewart (1977)
Black Vulture	13	No	?	Stewart (1983)
King Vulture	30	?	?	Newton (1979)

Thus taking the mass of an adult Cape Vulture to be in the range 8.0 to 9.5 kg (C.J. Brown, *in litt.*; Mundy 1982: 26; pers. obs.) and inserting into the equations of Lindstedt & Calder (1976) yields estimates of longevity, T = 24.1 to 24.9 years for wild birds and T = 42.0 to 43.4 years for captive birds. It can be seen that these two estimates are consistent with the observed longevities of similarly size scavengers (Table 5.2).

On the basis of a mathematical model devised it has been estimated that California Condors must have survived for at least 40 to 50 years in order to balance the population (Mertz 1971: 447). This suggests that scavengers of low reproductive output may have to live to their 'potential' maximum lifespan in order to replace themselves. The word 'potential' is used in the context of the formulae of Lindstedt & Calder (1976). It may be that these formulae underestimate the true longevities of these extremely K-selected birds.

Estimates of Longevity in the Cape Vulture

The oldest Cape Vulture to be found with a ring on it was 14 years old Vernon (1975), Ledger & Mundy (1977). The oldest colour-ring resighted is at least 10 years old at Potberg. These longevities fall far short of the potential maximum lifespan and this may be a reflection of the low number of recoveries (<600), the poor quality of the rings used (see section 5.2.2 below), and the paucity of observations of colour-ringed birds, especially outside the south-western Cape.

It will be seen when the population dynamics of this species are modelled (see below, Chapter Seven) that the previous estimates of the survival parameters are so low that the population should have declined to extinction during the time I have taken to collect and analyze these data! By gathering together all the ringing, recovery and resightings data generated since the previous analyses by Piper, Mundy & Ledger (1981) and Robertson (1984) it will be shown (see sections 5.2.3 and .4 below) that it is possible to provide estimates of survival which have much more optimistic implications.

5.2 Survival estimates from marked birds

For the Cape Vulture the process of death, unlike birth, is not concentrated in space or time and so is not observable directly. To estimate the rate at which birds die, as a function of age, time and spatial location, it is necessary to consider methods other than the direct observation of non-identifiable individuals. To estimate survival, over 7000 Cape Vultures have each been fitted with a uniquely numbered metal ring (see section 5.2.1 below). Nearly 600 of these marked birds have been found dead (i.e. 'recovered') and reported to the original ringers (raw data may be found in Piper, Mundy & Mundy, in prep.). Techniques for estimating survival from these ring-recovery data are reviewed here (for computations see section 5.2.3 below).

It will be seen in this chapter that the analysis of ring-recovery data is fraught with difficulty, and so an alternative method of estimating survival is investigated: resightings of colour-marked birds (but see new references and remarks at the end of the second paragraph on page 210). From 1973 many Cape Vulture nestlings were also fitted with up to five colour rings in addition to the metal ring. This gave most birds a unique identity (to the human observer, that is) which made it possible to census marked birds from afar. Unfortunately, the members of the Vulture Study Group did not exploit fully this potential source of data (pers. obs.), except for the small population in the south-western Cape (A.F. Boshoff & H.A. Scott *pers. comm.*). The resightings of colour-ringed birds in the south-western Cape will be used to provide estimates of survival (for computations see section 5.2.4 below).

Both recoveries of dead, marked birds and resightings of uniquely identifiable birds contribute information about survival. It is thus to be hoped that these two data-sets can be combined to provide less biased, and more robust estimates of survival. A similar problem exists in studying survival among human cancer patients. A technique called the 'proportional hazards model' (McCullagh & Nelder 1989: 421 ff.) has been devised for that problem and it is hoped to be able to use this new method for the analysis of the joint ring-recovery and ring-resighting data-set (L.G. Underhill *pers. comm.*).

Estimating survival from ring-recoveries

Assumptions

A number of assumptions are made when constructing fully stochastic models of survival using ring-recovery information. Chief among these are the forms the survival and reporting rates are supposed to assume. In particular, survival may be assumed to be predominately age-specific or time-specific, or even both. Most of the earlier models, up until the late 1970s, assumed that the reporting rate was independent of age, year and spatial location (Burnham & Anderson 1979).

Most models based on the so-called 'life table' philosophy start with the following assumptions (Anderson, Burnham & White 1985: 228).

1) The ringed sample is representative of the population of interest.
2) There is no loss of rings.
3) Survival rates are not affected by ringing.
4) The date of recovery for those birds recovered is correctly reported and recorded.
5) The fate of each ringed bird is independent of the fate of other ringed birds.
6) Annual survival is a function of age only and is independent of year.
7) The reporting rate is a constant for all age classes and years.
8) Every ringed bird experiences homogeneous survival and reporting rate parameters, i.e. there are no population subgroups having heterogeneous parameters.

There are other ways of formulating survival models which are more robust or more amenable to statistical tests of adherence to assumptions (see Brownie, Anderson, Burnham & Robson 1985). However, in setting up estimation procedures it is important to understand the underlying biology of the species being studied (Anderson & Burnham 1987).

Failure of assumptions

There is a large class of models in which it is assumed that survival is a function of age only (i.e. independent of year) and the reporting rate is constant for all ages and all time. These models have been applied to a wide range of species, but it has been shown that many of these data-sets do not meet the underlying assumptions (Anderson, Wywialowski & Burnham 1981). Two statistical procedures have been devised to test recovery data-sets for their adherence to the full range of assumptions usually made in ring-recovery models (Burnham & Anderson 1979: 359-360), as well as to the assumption that the first year recovery rate is constant (loc. cit.: 360). In an examination of ten ring-recovery data-sets of non-hunted species, it was found that six of the ten did not satisfy the underlying assumptions (Anderson, Wywialowski & Burnham 1981). For an analysis of 45 recovery data-sets from hunted waterfowl in North America it has been found that the majority did not meet the underlying assumptions (Burnham & Anderson 1979). Unfortunately, most models for estimating survival are not robust to failure of assumptions (loc. cit.) and in most cases the estimates of first year survival are negatively biased.

It is assumed (often only implicitly) that the process of ringing does not change the subsequent survival and reporting rates, but this is not true for some species, especially those which are hunted (Aebischer & Coulson 1987).

Recoveries are usually assumed to be reported soon after the bird was found dead. In species which are exploited this assumption is sometimes violated, which causes estimates of survival to be positively biased (Anderson & Burnham 1980).

Rings are assumed to last the full lifetime of the bird, but ring loss has been serious in some species and causes survival to be underestimated (Anderson & Burnham 1980).

A number of techniques have been developed for deriving numerical estimates of survival from 'life table' type models (Lebreton 1977; White 1983: program SURVIV). These models have more parameters to be estimated than degrees of freedom (Anderson, Burnham & White 1985: 230) so that it necessary to make assumptions about one or more parameters, in order to ensure that estimation with the model is possible. The usual assumption is that all age-specific survival rates, above a certain age, are constant. However, this assumption, which is an identifiability constraint, can lead to significant bias in estimating survival rates, even when there are only small deviations from this assumption (Lakhani & Newton 1983). It has been suggested that '... all hitherto published estimates of age-specific survival are liable to be untrustworthy, if they are based solely on recoveries of dead birds' (loc. cit.). The estimates of survival derived for the Cape Vulture (Piper, Mundy & Ledger 1981) are not uniquely estimated (Anderson, Burnham & White 1985: 232). In fact, it can be shown that the recovery rate for first year Cape Vultures increases with time (loc. cit.: 233). To overcome the 'identifiability' problem, it has been suggested that in addition to ringing nestlings a reasonable number of birds aged one as well as adult birds should also be ringed (Clobert & Lebreton 1991: 83 and references therein) - but this is difficult for the Cape Vulture because of logistic and financial constraints. Alternatively, instead of assuming that survival varies as a function of time, assume that it varies as some function of an environmental parameter (e.g. winter temperature was used in a model of Grey Heron survival, North & Morgan 1979; see also Freeman & North 1990; Rinnie, Lokki & Saurola 1990). While this is a possibility for the Cape Vulture there is as yet no suggestion that this species' survival varies with any environmental parameter[1]. Furthermore, the range of this species is so large that it is doubtful whether any one such environmental parameter could be applied to all individuals in the population.

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[1] In a review of this Chapter Mundy (*in litt.*) suggests that rainfall is a possible candidate: "If rainfall is poor, i.e. drought, then ungulates and herbivores will increasingly die and more Cape Vultures will survive. Conversely, if rainfall is good, then more first-year Cape Vultures will die. I suggest an examination of the relationship between ring-recoveries and rainfall".

The reporting rate is usually assumed to be constant across all age-classes and for the whole of the study period but it can differ between age-classes (e.g. 9.4% for first year Tawny Owls vs 24.1% for older birds, Rinnie, Lokki & Saurola 1990). Notwithstanding this example, most studies have shown that the reporting rate for first-year birds is higher than that for older birds (Brownie, Anderson, Burnham & Robson 1985: 112).

Models

A wide variety of models has been proposed for estimating survival (see reviews in Brownie, Anderson, Burnham & Robson 1985; Burnham, Anderson, White, Brownie & Pollock 1987; Clobert & Lebreton 1991; North 1987, 1990; Seber 1982, 1986). The model employed generally depends on the number and nature of the assumptions. If it is assumed that survival is a function of year, but it is independent of age and the reporting rate is constant, then the method of Aebischer (1987) may be used. A set of flexible models has been constructed in which the reporting rate is allowed to vary with both time and age-class (Freeman & Morgan 1990, 1992; Morgan & Freeman 1989) and these may have some applicability in the study of Cape Vulture survival.

A model for one age-class in which survival is allowed to vary with year has been constructed (Conroy & Williams 1984). This model allows the time-specific variation to be tied to an environmental variable (see North & Morgan 1979).

Models have been developed which allow the survival to be heterogeneous (Pollock & Ravelling 1982).

A flexible and powerful program for use in estimating survival (MULT - Conroy & Hines 1990) has been developed and compared favourably with SURVIV (developed by Brownie, Anderson, Burnham & Robson 1985

Many criticisms have been levelled at the attempt to estimate survival from ring-recovery data, but 'Finally we have to remember that these data are often the only way to estimate survival rates of young' (Clobert & Lebreton 1991: 83).

Estimating survival from ring-resightings

In principle, there is no difference between identifying a bird from the resighting of its colour rings or from capturing it and reading the mark (i.e. ring number) directly. The differences come in the nature of the biases encountered in the sampling.

The primary advantage of using ring-recapture and ring-resighting data over ring-recovery data is the greatly increased quantity of data available for analysis and this often leads to less biased estimates of survival (e.g. Peach, Buckland & Ballie 1990).

From the 1960s there has been an increasing interest in the development of statistical models for the analysis of data from ring-recapture (also called band-recapture and capture-recapture) experiments. Initially this interest was directed at elucidating population size (e.g. Begon 1979) and later at estimating survival (e.g. Cormack 1989 and references therein). The standard method of estimating survival from colour-ring resighting data (Cormack 1964) has been shown to be functionally identical to the survival component of the Jolly-Seber model (Clobert & Lebreton 1991: 84 and references therein). A range of estimation procedures is available. General purpose packages such as GLIM (Cormack 1989) and its equivalents GENSTAT and SAS (Burnham 1989) can be used. In addition, several special purpose programs have been written: ESTIMATE (Brownie, Anderson, Burnham & Robson 1985), JOLLY (Brownie, Hines & Nichols 1986), SURGE (Lebreton & Clobert 1986; Pradel, Clobert & Lebreton 1990; this software has just been updated - November 1993; J.-D. Lebreton pers. comm.), MULT (Conroy & Hines 1990) and RELEASE (Burnham, Anderson, White, Brownie & Pollock 1987); the latter program being used to test goodness-of-fit. A comprehensive review of some of these programs is provided by Brownie, Anderson, Burnham & Robson (1985: 153-154).

Survival rate can be estimated as a function of calendar year and sex if there are sufficient observations (e.g. Ebbinge & van Biezen 1987). In some well-studied populations of colour-ringed birds, it has been observed, that certain individuals are seen less frequently than others and this lowered probability of being resighted leads to the estimate of survival being negatively biased (e.g. Ebbinge & van der Voet 1990).

The sampling biases encountered when using resightings as opposed to recaptures are often different and need to be understood when estimating survival. A comparison of these two sampling techniques has been made by Elder & Zimmerman (1983) for a North American *Parus* species.

While it is likely that the use of ring-resighting data will yield less biased estimates of survival than ring-recovery data they require much more intensive fieldwork and also suffer from a number of defects The two most important (Clobert & Lebreton 1991: 85) are listed below.

2) Survival rates will be negatively biased if there is any emigration because all permanent emigrants are counted as deaths.

If the probability of capture and survival varies with age then this should be incorporated into the model (Pollock 1981).

Simultaneous use of recoveries and recaptures

The simultaneous use of ring-recovery and ring-recapture data has been recommended (Buckland 1980; Clobert & Lebreton 1991: 85; Mardekian & McDonald 1981) as a way of overcoming the weaknesses of each technique when used individually.

Other methods of estimating survival

Sometimes it is possible to use a well defined polymorphism within a population to estimate survival (e.g. Birkhead, Kay & Nettleship 1985) but this is not applicable to the Cape Vulture due to no known visible polymorphism. It has been suggested that from the stable age distribution of a population it may be possible to make inferences about adult survival rates (see the review in section 5.1 above). It is felt that this technique is too imprecise for use with the Cape Vulture (Piper, Mundy & Ledger 1981: 822), though it has been tried with African Whitebacked Vultures (Houston 1974). There has been little use of long-term or long-range radio-tracking or radio-telemetry data in the Cape Vulture (see Boshoff, Robertson & Norton 1985). If this does happen then appropriate analytical methods should be employed (e.g. Bunck 1987; Heisey & Fuller 1985; Lakhani 1990; Pollock, Winterstein & Conroy 1989).

Table 5.1

Number of Cape Vultures ringed with ' B' prefix rings.

	Site	
Year	Roberts' Farm	Totals
1950	11	11
Totals	11	11

Table 5.2

Number of Cape Vultures ringed with ' C' prefix rings at each site in each calendar year.

Year	Site Kranzberg	 Potberg	 Roberts' Farm	 Skeerport	Totals
1948	31	0	0	0	31
1950	0	0	78	0	78
1951	0	2	0	0	2
1957	0	0	0	17	17
1961	0	0	0	46	46
Totals	31	2	78	63	174

5.2.1 The number of marked Cape Vultures

Putting a unique mark on a bird means that it may be possible to track that bird through space and time and so make inferences about its survival. Four questions need to be considered here.

1) How many Cape Vultures were ringed?
2) When were they ringed?
3) Where were they ringed?
4) What types of rings were used?

When the ringing of Cape Vultures began in 1948 (Ashton 1979) the birds were fitted with metal rings manufactured from aluminium. The mark on a metal ring is composed of a ring prefix of up to three letters (or digits) and a five digit number pre-filled with zeros. The prefixes on rings made of aluminium were ' B', ' C', '508', '509', '548' and '658'. The last of these aluminium rings was fitted in 1969 by which time 3198 had been used. It became clear after some time that the aluminium rings were not lasting and this necessitated a switch to monel rings (designed for penguins and bearing the prefix ' G'); this began in 1969. From 1970 all Cape Vultures were fitted with these new rings and by 1990 a total of 4091 birds were fitted with these new rings. Thus a grand total of 7 289 Cape Vultures have been fitted with metal rings. From 1983 the Vulture Study Group ceased its blanket ringing campaign. The distribution of rings used across all colonies over the period 1948 to 1984, both years included, has been tabulated (Tables 5.1 to 8).

Table 5.3

Number of Cape Vultures ringed with '508' prefix rings at each site in each calendar year.

	Site					
Year	Kranzberg	Mn	Potberg	Rb	Skeerpoort	Totals
1951	0	0	0	77	0	77
1952	15	0	0	62	0	77
1953	0	0	0	119	8	127
1954	0	0	0	97	30	127
1955	0	0	0	36	12	48
1956	0	0	0	109	39	148
1957	10	0	0	161	19	190
1958	0	0	0	111	34	146
1959	0	0	1	42	80	123
1960	0	0	3	52	177	232
1961	0	0	0	34	0	34
1962	0	0	0	51	29	80
1963	0	1	0	0	100	101
1964	0	5	0	0	0	5
1967	0	0	0	0	7	7
1968	0	0	0	0	2	2
Totals	25	6	4	951	537	1523

Notes: Mn = Mannyelanong and Rb = Roberts' Farm

Table 5.4
Number of Cape Vultures ringed with '509' prefix rings at each site in each calendar year.

Year	Site Mn	Potberg	Roberts' Farm	Skeerpoort	Nooitgedacht	Totals
1955	0	0	41	0	0	41
1957	0	0	0	69	0	69
1958	0	0	10	0	0	10
1959	0	0	8	0	0	8
1960	0	0	11	0	0	11
1961	0	0	17	0	0	17
1962	0	0	0	85	33	118
1963	87	0	50	0	22	159
1964	59	0	37	161	0	257
1965	0	6	0	113	0	119
1966	0	0	0	11	0	11
1967	0	0	0	72	0	72
Totals	146	6	174	511	55	892

Note Mn = Mannyelanong

Table 5.5
Number of Cape Vultures ringed with '546' prefix rings in each calendar year.

Year	Site Skeerpoort	Totals
61	69	69
63	20	20
68	4	4
69	34	34
Totals	127	127

Table 5.6

Number of Cape Vultures ringed with '658' prefix rings at each site in each calendar year.

	Site				
Year	Mannyelanong	Roberts' Farm	Skeerpoort	Unknown	Totals
66	0	6	122	0	128
67	10	38	37	1	86
68	0	0	100	0	100
Totals	10	44	259	1	314

Table 5.7

Number of Cape Vultures ringed with 'G' prefix rings at each site in each calendar year for the period 1984 to 1990.

	Year						
	84	85	86	87	88	90	Totals
Aasvogelvlei	4	6	8	4	0	0	22
Kommandonek Rest	1	0	0	0	0	0	1
Potberg	6	7	7	6	1	1	28
Sparta Baby Beef	1	0	0	0	0	0	1
Skeerpoort	0	0	0	0	0	14	14
Manoutsa	0	0	0	0	0	1	1
Totals	12	13	15	10	1	1	67

Table 5.8
Number of Cape Vultures ringed with 'G' prefix rings at each site in each calendar year

Site	'69	'70	'71	'72	'73	'74	'75	'76	'77	'78	'79	'80	'81	'82	'83	'84	Totals
Aasvogelvlei	0	0	0	0	0	0	0	0	0	0	0	0	6	6	4	0	16
Baratani Hill	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3
Bellair (CROW)	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	3
Colleywobbles	0	0	0	0	0	0	0	40	18	70	57	34	102	58	39	0	418
Debshan Shangani	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Dronfield	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	4
Giant's Castle	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0	12
Gonarezho	0	0	0	0	0	2	9	0	0	0	0	0	0	0	0	0	11
Karnmelkspruit	0	0	0	0	0	0	0	0	0	0	0	17	0	0	0	0	17
Mannyelanong	0	0	0	0	2	27	55	61	55	52	51	27	38	39	23	0	430
Manoutsa	0	0	0	0	0	0	14	35	24	32	53	48	46	64	47	0	363
Manyana	0	0	0	0	21	13	13	5	0	0	0	0	0	0	1	0	53
Mlengana	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Pilansberg	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	3
Potberg	0	0	0	14	14	22	15	11	13	7	9	6	7	10	5	0	133
Roberts' Farm	0	29	30	40	105	106	132	110	98	66	66	73	51	90	111	0	1107
Sengwa	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Skeerpoort	82	60	101	7	81	133	136	130	157	107	125	62	92	91	68	0	1432
Tuli Block	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Unknown	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2
Waterberg	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	3
Zastron	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	8
Totals	83	91	131	63	224	308	386	392	365	334	363	280	345	358	301	1	4024

5.2.2 The nature of the ring-recovery-reporting process

If a population demographer could create an 'ideal' population to study it would have each and every individual uniquely identifiable when it entered the world and its death would be recorded when it left the world. To achieve this, in the real world of the Cape Vulture, as many nestlings as possible are fitted with rings when in the nest. When they die it is hoped that each dead bird, with its unique ring, will be recovered by a member of the public. If a fixed proportion of dead birds bearing rings were found (i.e. recovered), and if a fixed proportion of the recovered birds were reported to the ringer, then it would be possible to estimate survival directly. Unfortunately, the process of finding and reporting dead, ringed birds is complex and is confounded with the causes of mortality. If it is possible to develop a clear understanding of the nature of this ring-recovery-reporting process then it should be possible to model it more accurately and so eliminate the reporting-rate component, as a set of 'nuisance parameters' and hence derive better estimates of survival. To this end, a conceptual model is provided for the process of ring-recovery and reporting in the Cape Vulture. One motivation for the development of this model comes from the criticism by Anderson, Burnham & White (1985) of an earlier analysis of Cape Vulture ring-recovery data (Piper, Mundy & Vernon 1981) it which its was shown that a number of underlying assumptions of the ring-recovery-reporting model were not met.

There are many steps in the ring-recovery-reporting process and these are enunciated below (see Figure 5.2) in terms of the major phases through which a bird and its ring pass, from initial ringing to final recovery and reporting.

Ringing

The ring-recovery-reporting process starts when a ring is placed on a nestling. For Cape Vulture nestlings there is no reason to believe that the nestlings are not chosen at random from the population (i.e. within a given breeding colony), at least with respect to their ability to survive, disperse, die and have their rings reported. It is likely that this assumption of randomness is not true for birds caught once they have fledged. A study of ducks caught after they had become free-flying birds in Britain showed that they had higher mortalities in the first year after capture and ringing (Aebischer & Coulson 1987). Hence any bird not ringed as a pullus in the nest is to be excluded from these analyses.

Fledging

Once a nestling has been ringed there are four possible things which can happen to it. First, the nestling can die and be found with its ring. Second, the nestling can die and its carcass can disappear (e.g. devoured by a porcupine, P.J. Mundy *pers. comm.*) so that only its ring can be found. Third, the nestling can die and it, together with its ring, can be totally lost. Finally, the nestling can fledge successfully. If a dead bird is found with its ring still attached then it may be possible to infer from its plumage, and the wear on the ring, if it fledged before dying, or if it died as a nestling (i.e. without fledging). But if only the ring is found it may not be possible to decide if the nestling fledged.

Dispersal

Once a nestling has successfully left the nest it is said to have fledged (Campbell & Lack 1985: 218). There are four things which can happen to a ringed fledgling.

1) The fledgling can die at its natal colony and be found with its ring.
2) The ring may be found with no trace of the dead bird's body.
3) The bird and its ring can be totally lost.
4) The fledgling can successfully disperse away from its natal colony.

The process of dispersal could occur up to five months after fledging, because Cape Vultures may have an extended post-fledging dependence period (PFDP) as has been seen from nestlings ringed at the Potberg colony (Robertson 1984). If only the ring is found and it shows no signs of wear, then it may not be possible to decide if the pullus did in fact fledge. In cases of doubt, the ring is assumed to come from a nestling rather than a fledgling.

Ring loss

A critical assumption when using marked birds to estimate survival is that the marks are never lost. However, a ring can be lost at any stage of a bird's life - from the time it is ringed in the nest and thereafter until its death. Ring loss is likely to increase the longer the ring has been on the bird. In a number of studies of terns ring loss has been convincingly documented (e.g. Hatch & Nisbet 1983a, b; Ludwig 1981; Nisbet & Hatch 1983), especially after 20 years (Bailey, Woolfenden & Robertson 1987). But not all the rings that fall off are lost, sometimes the lost ring may be found. For the Cape Vulture, there is a recovery for which the 'ring dropped off during a fight', and isolated rings have been found below the cliffs on which the birds were ringed and reported as 'gaping open'. But, I suspect that most rings which drop off a bird are never found. Ring loss is a 'significant problem only with long-lived species experiencing especially severe band loss' (Nelson, Anderson & Burnham 1980: 270; Seber 1982: 526). This causes estimates of survival to be negatively biased (Kremers 1988). From observations of aluminium rings on Redshanks *Tringa totanus* it was found that their rings lost 10% of their mass p.a. (Zmud 1985) while monel rings fitted to Shorttailed Shearwaters *Puffinus tenuirostris* (Wooller, Skira & Serventy 1985) lost only 1.2% p.a. These two loss-rates may not be strictly comparable because the ring sizes are different (about 3 mm vs 11 mm) and so have different surface to volume ratios which will influence the rate at which they corrode. However, it would seem likely that the aluminium rings initially fitted to Cape Vultures would have had a higher weight loss than the monel rings fitted from the 1970s onwards and thus it is likely that the aluminium rings would have been lost at a higher rate than the monel rings.

Dead bird with ring

Once a ringed bird has died there are two possible outcomes. It may or may not be found. There are three reasons as to why a ring may not be found. First, the dead bird and its ring may not be 'findable' (e.g. it drowned in a river). Second, the ring may be 'findable' but there is no one to look for it (e.g. on the screes of a seldom visited roost or colony). Finally, the ring may just not be found. On the other hand the ring, with or without the dead bird, may be found.

A found ring

Once a ring is found there may be four different reasons for not reporting it. First, the ring is not recognised as an object to be returned (e.g. the person may not belong to a culture in which such things are well established). Second, the ring is deliberately withheld because the bird was killed by a person who knows that this is illegal and wishes to conceal the fact. Third, the ring may be withheld for cultural reasons (Ash 1976; referring to Ethiopia):

> "Many ringed birds found by illiterate people are not reported, they say that 'as it [the bird's ring] must have been put on by God we sent it back to Him'!"

Fourth, the ring is withheld because of financial constraints (e.g. the finder cannot afford the packaging and postage) or because the finder is not literate.

The ring is returned

If a ring is indeed found and reported there are two ways in which the recovery may not be useful. First, the number or mark is unreadable (though it may sometimes be possible to restore the legibility of a worn or abraded ring, Aebischer 1983). Second, the number or mark is incorrectly recorded and the physical evidence is lost (e.g. a number of Cape Vultures are reported to the southern African ring address 'Pretoria Zoo' as having the ring prefix '6', not 'G'; T.B. Oatley, SAFRING *pers. comm.*). Alternatively the ring may be reported in good condition and so signal that the bird is indeed dead.

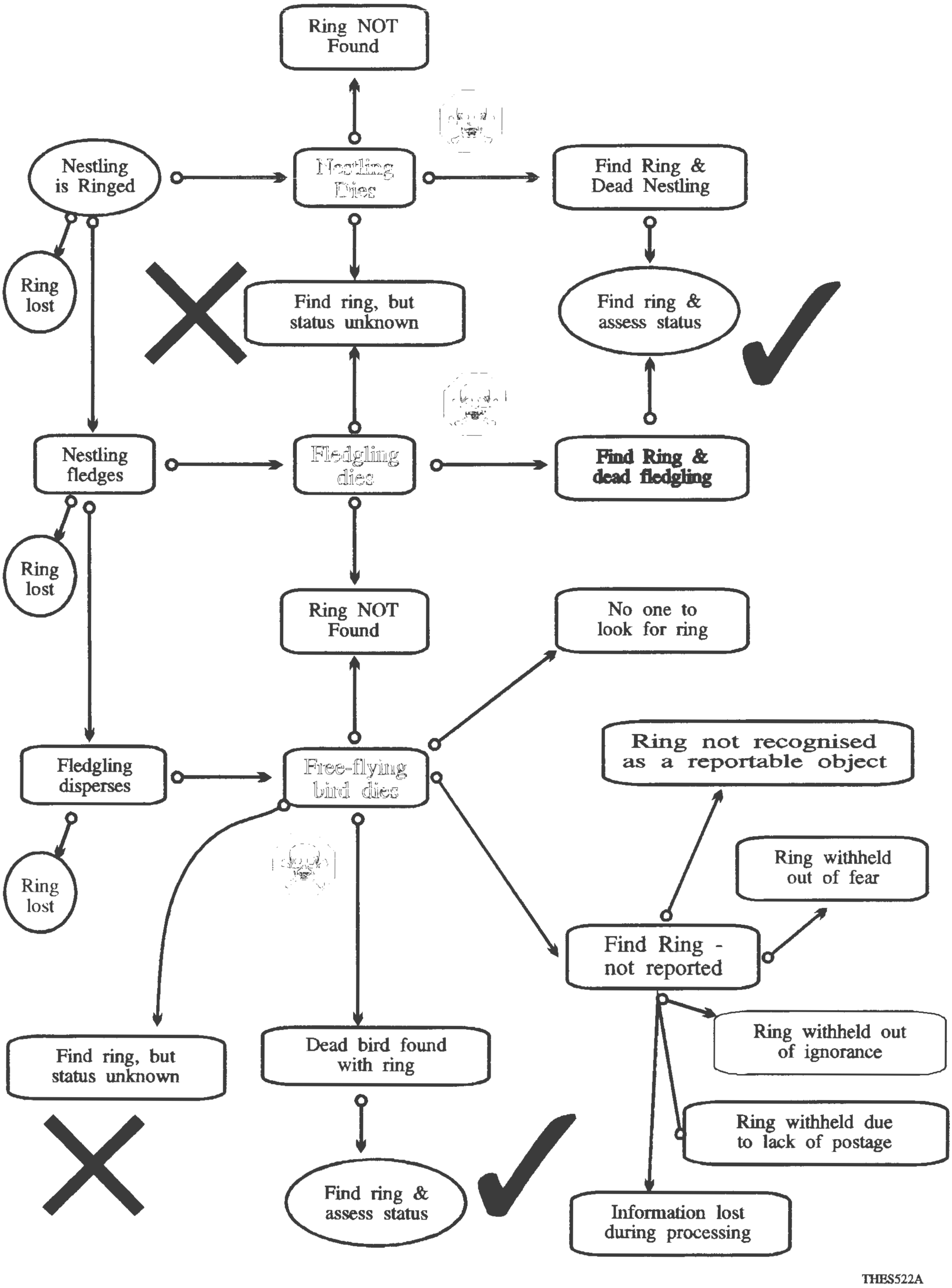

Figure 5.2 Schematic model of ring-recovery-reporting process

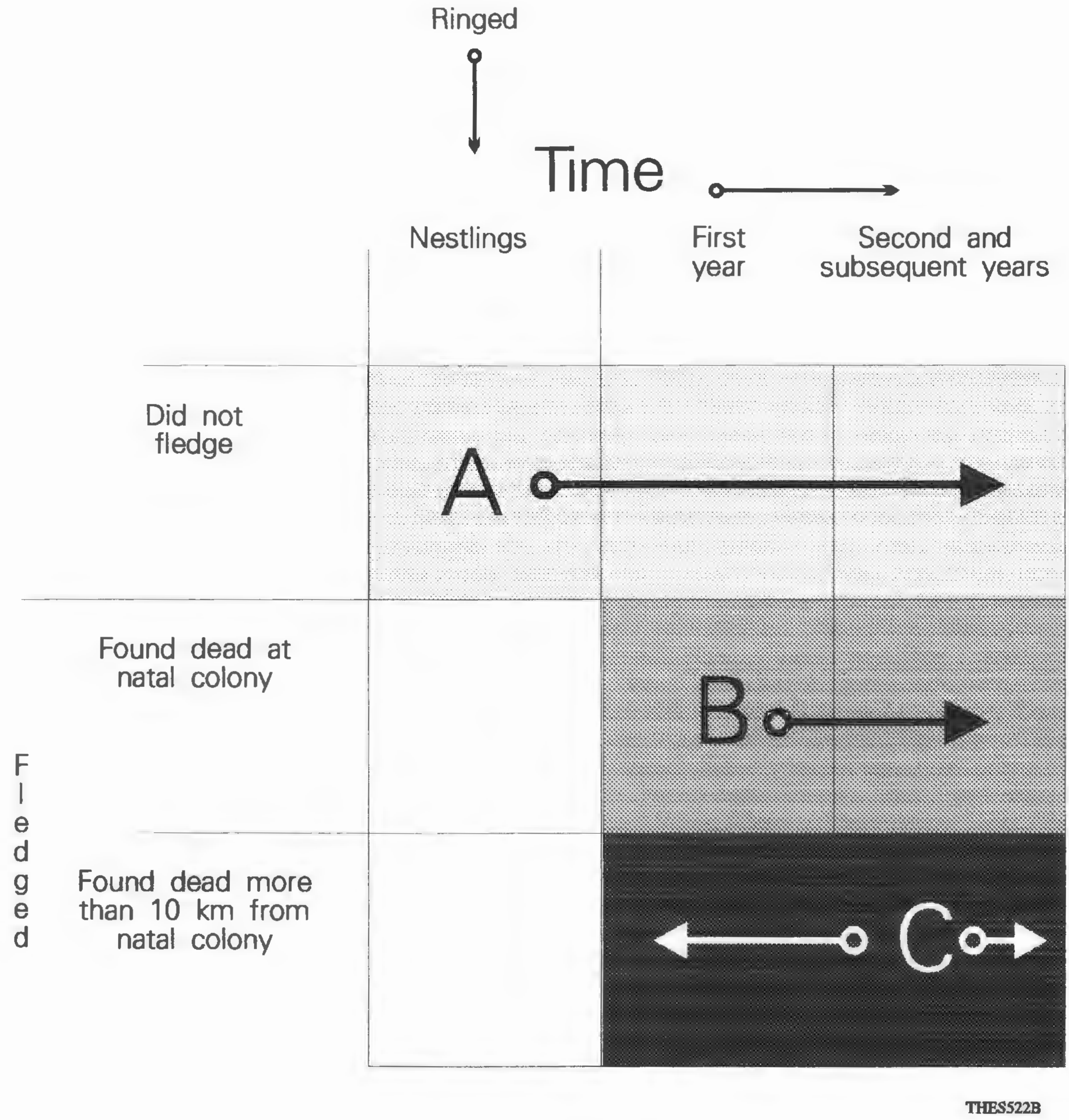

Figure 5.3 Three categories of ring-recovery.

Given that a recovery is reported it is likely that the probability of this happening will be a function of the place, season, year and cause of death as well as the bird's age at death (Baillie & Green 1987; Conroy 1983; Kania & Bussee 1987). The probably that a ring is reported may also be higher if the bird is carrying one or more colour rings as well as the metal ring (Shedden, Monaghan, Ensor & Metcalfe 1985).

To investigate these processes a subset[1] of 575 recoveries (total = 582) from 7118 nestlings ringed (total = 7289), recovery rate = 8%, have been divided into three categories:

	Nonsignificant recoveries.		*Significant[2] recoveries*
A)	Dead nestlings or Age indeterminable	B)	Definitely fledging, or older, dead at natal colony
		C)	Died away from natal colony

A bird is deemed to have died away from its natal colony if the place at which it was found is at least 10 km from the place at which it was ringed. This tolerance is used to allow for the mis-recording or misidentification of ringing and recovery localities. This was particularly common in the early days of the project; by way of example, recoveries of Cape Vultures were entered as having been found 'at the same place' (implying the place of ringing). The use of alternative names for the same place and the use of the same name for nearby places was once also common. When only the ring-number was reported as having been found at the foot of the natal colony but the ring was not forwarded to the Vulture Study Group for assessment of 'wear', it is not possible to determine the bird's age at death so that the recovery is allocated to the category 'Age indeterminable'. These categories may be viewed in relation to their age at death and dispersal distance (Figure 5.3). In the above categorization recoveries have been divided into *nonsignificant* and *significant*.

Modelling the reporting rate

A number of ideas as to possible sources of inhomogeneities in reporting rates have been postulated. These are tested using a series of generalized linear models (GLM) fitted using GENSTAT 5.1 (Anon. 1988: 347 ff.). The 7118 (excluding 171 birds, see footnote 1 below) ringed Cape Vultures have been grouped into 178 uniform groups within which they are identical with respect to: Ring prefix, Colony, Year and Colour rings (Table 5.9). For each group the number of birds ringed and the number of significant recoveries is treated as a binomial response variable in a GLM using the logit transform as the link function. Each of the four putative sources of reporting rate inhomogeneity is tested independently. In this

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[1] A few sites at which only a handful of nestlings were ringed have been excluded.

[2] The term 'significant' is used to indicate that the ring carries useful information - either as to longevity or distance travelled - its usage corresponds with that of the southern African ring-clearing organisation, SAFRING and its European counterpart, EURING (T.B. Oatley, SAFRING *pers. comm.*).

analysis the 273 significant recoveries are used as only they contain information pertinent to estimating survival (the nominal reporting rate for significant recoveries is 273/7118 = 3.8%). A fundamental assumption of these analyses is that the recovery process is complete, i.e. all the birds that are going to die and be reported have already died. The last significant ringing took place in 1983 (Table 5.8) and as most recoveries are reported in the first five years of life, this is a reasonable assumption.

The effects of ring prefix

Seven different ring series were used, each with its own ring prefix. Is there any difference in reporting rate between them? It is hypothesized that there should be because the early rings were made of aluminium and it is thought that they were more readily lost from birds than the ‘G’ prefix monel rings. The number of recoveries, n_i from the N_i nestlings ringed in the i^{th} group (each line in Table 5.9 is a ‘group’) may be modelled as a binomial response variable in a generalized linear model (GLM) using a logit link function (see motivation in Chapter Three). The reporting rate, $r_i = n_i/N_i$ is modelled as follows:

$\text{Logit}(r_i) = \text{Ln}\{r_i/(1-r_i)\} = a_0 + a_1\{\text{‘B’ prefix used}\} + a_2\{\text{‘C’ prefix used}\} \ldots$

The coefficients (i.e. a_0, a_1, a_2 ...) are shown below along with the sample size (i.e. appropriate the number of lines in Table 5.9), the standard error (s.e.), t-value, probability (Prob. - approximate measure of how different the coefficient is from 0) and the reporting rate for that component.

Component	*N*	*GLM Estimate*	*s.e.*	*t*	*Prob.*	*Reporting rate*[3]
‘ B’	1	-2.30	1.05	-2.20	**1.5%**	9.1%
‘ C’	5	-2.85	1.45	-1.97	**2.5%**	0.6%
‘508’	112	-1.60	1.06	-1.51	6.6%	1.9%
‘509’	30	-1.31	1.07	-1.22	11.2%	2.6%
‘546’	20	-6.55	4.63	-1.42	7.9%	0.01%
‘658’	4	-0.76	1.08	-0.70	24.2%	4.5%
‘ G’	6	-0.64	1.05	-0.61	27.1%	5.0%

(Statistically significant coefficients are shown in bold.)

The deviance of the residuals is 175.8 with 171 degrees of freedom (mean deviance = 1.028) and the associated probability value (assuming asymptotic chi-square) is 38.5%, i.e. this model adequately fits the data. There are 12 points with high leverage (i.e. Nos. 1, 2, 4, 6, 32, 51, 52, 57, 63, 64, 65 and 66 - see Table 5.9). Of these, data item 1 is the only observation for the ‘ B’ ring prefix, items 2, 4 and 6 are for ‘ C’ prefix rings while all the other data-points are from sites with large numbers ringed. It can be seen that both ‘ B’ and ‘ C’ prefix rings have Student’s t-values which are statistically significant: ‘ B’ prefix rings are over-reported and ‘ C’ prefix rings are under-reported.

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[3] These intermediate GLM results are not given the status of ‘Table’ as they not referred to elsewhere in the thesis.

The effect of using an Aluminium Ring

From the preceding analysis it may be seen that five of the aluminium ring series (i.e. ' C', '508', '509', '546' and '658') have a lower reporting rate than the monel ring. To test this the rings were separated into monel and aluminium.

Component	*N*	*GLM Estimate*	*s.e.*	*t*	*Prob.*	*Reporting rate*
Monel	112	-2.9387	0.0724	-40.60	**0.00%**	5.03%
Aluminium	66	-0.811	0.139	-5.82	**0.00%**	2.30%

(Statistically significant coefficients are shown in bold.)

The deviance of the residuals is 192.6 with 176 degrees of freedom (mean deviance = 1.095) and the associated probability value (assuming asymptotic chi-square) is 18.6%, an acceptable goodness-of-fit. There are 15 points with high leverage (i.e. Nos. 15, 18, 19, 20, 32, 34, 51, 52, 64, 66, 144, 163, 165, 167 and 168 - see Table 5.9). The first ten observations listed above (i.e. 15, 18, ... 66) are all large samples of aluminium-ringed birds while the remaining five (i.e. 144, 163, ... 168) are large samples of monel-ringed birds. Thus it may be seen that there is a significantly lower reporting rate for aluminium rings, in fact they have half the reporting rate. The direction of this difference was expected, but not its magnitude.

The reporting rates from different colonies

It is suspected that the reporting rates from some colonies will be higher than others because they are visited more often and situated in regions that are well populated by people who are predisposed to reporting recoveries (only the 11 colonies in the following list were investigated - there were too few birds ringed at the other sites listed in Tables 5.2 to 5.8).

Component	*N*	*GLM Estimate*	*s.e.*	*t*	*Prob.*	*Reporting rate*
Aasvogelvlei	7	-2.428	0.602	-4.03	**0.4%**	8.1%
Colleywobbles	10	-0.299	0.637	-0.47	31.9%	6.1%
Karnmelkspruit	1	-5.17	6.61	-0.78	21.8%	0.05%
Kranzberg	3	-0.849	0.939	-0.90	18.5%	3.6%
Mannyelanong	22	-0.779	0.639	-1.22	11.2%	3.9%
Manoutsa	11	-1.501	0.713	-2.11	**1.8%**	1.9%
Manyana	7	-0.811	0.938	-0.86	19.5%	3.8%
Nooitgedacht	2	-1.56	1.18	-1.33	9.3%	1.8%
Potberg	20	-0.137	0.673	-0.20	42.1%	7.1%
Roberts' Farm	44	-0.824	0.612	-1.35	8.9%	3.7%
Skeerpoort	51	-0.848	0.610	-1.39	8.3%	3.6%

(Statistically significant coefficients are shown in bold.)

The deviance of the residuals is 212.8 with 167 degrees of freedom (mean deviance = 1.274) and the associated probability value (assuming asymptotic chi-square) is 1%; not an acceptable goodness-of-fit. Thus colony of ringing is not an adequate descriptor of reporting rate variation. There are 13 points with high leverage (i.e. Nos. 2, 7, 8, 39, 40, 72, 76, 80, 84, 111, 114, 115 and 117 - see Table 5.9). These observations are influential because they come from the colonies at which ringing has taken place on only a few occasions: observations 2, 7 and 8 at Kranzberg, observations 39 and 40 at Nooitgedacht, observation 72 at Aasvogelvlei, observations 76 and 80 at Colleywobbles, observation 84 at Kranzberg, observation 111 at Manoutsa and observations 114, 115 and 117 at Manyana. There is one point with a significant residual (i.e. No. 34 - see Table 5.9), this for 100 birds ringed at Skeerpoort with no recoveries while the reporting rate is 3.6% for this colony. The colony with the lowest reporting rate which is statistically significantly different from the rest is Manoutsa. This lower reporting rate may be indicative of their foraging in the Kruger National Park where there are few people on the ground to search for dead, ringed birds. The colony with the highest reporting rate which is statistically significantly different from the rest is Aasvogelvlei. This site was active during the 1980s when there was (and still is) an active monitoring programme (Boshoff & Scott 1990) and the assiduous searching may account for the higher reporting rate.

Comparing colonies in 'subsistence farming' areas with other areas

Colonies in 'subsistence farming' areas are surrounded by people with a low standard of living and little educational training. Do birds ringed at these colonies have a lower reporting rate?

Component	*N*	*GLM Estimate*	*s.e.*	*t*	*Prob.*	*Reporting rate*
Commercial farming	139	-3.2681	0.0682	-47.91	**0.0%**	3.7%
Subsistence farming	39	0.271	0.160	1.69	**4.6%**	4.8%

(Statistically significant coefficients are shown in bold.)

The deviance of the residuals is 227.3 with 176 degrees of freedom (mean deviance = 1.292) and the associated probability value (assuming asymptotic chi-square) is 1%; not acceptable goodness-of-fit. Thus this division does not provide a useful description of reporting rate variation. There are 16 points with high leverage (i.e. Nos. 37, 38, 74, 76, 77, 79, 80, 81, 83, 89, 91, 92, 93, 95, 98 and 99 - see Table 5.9). Of these influential points eight (i.e. Nos. 37, 38 ,89, ... 99) are for Mannyelanong which has a lower reporting rate (i.e. 3.9%) and the other eight are from Colleywobbles which has a higher reporting rate (6.1%) than that for the 'subsistence farming' category. In other words, the 'subsistence farming category' is not homogeneous with respect to reporting rate. There is one point with a significant residual (i.e. No. 69 - see Table 5.9), this for a 50% reporting rate (i.e. 2 out of 4) for Aasvogelvlei. This analysis shows that there is a significant difference in reporting rates between those colonies in subsistence and commercial famring areas.

The effects of fitting one, or more colour rings

It is known from other studies that the presence of a colour ring on a dead bird often calls attention to the numbered metal ring on the bird and so increases the reporting rate (Shedden, Monaghan, Ensor & Metcalfe 1985).

Component	*N*	*GLM Estimate*	*s.e.*	*t*	*Prob.*	*Reporting rate*
Metal ring only	104	-3.710	0.104	-35.56	**0.00%**	2.4%
Colour ringed	74	0.886	0.130	6.84	**0.00%**	5.6%

(Statistically significant coefficients are shown in bold.)

The deviance of the residuals is 180.5 with 176 degrees of freedom (mean deviance = 1.026) and the associated probability value (assuming asymptotic chi-square) is 39.2%, an adequate goodness-of-fit. There are 16 points with high leverage (i.e. Nos. 19, 32, 51, 142, 144, 145, 163, 165, 167, 168, 169 and 171 - see Table 5.9) and all these are from observations with a high number of birds ringed. The wearing of colour rings does indeed give rise to a statistically higher reporting rate, in fact twice as high. However, it must be borne in mind that colour rings (especially the old Darvic plastic rings fitted up until the late 1980s) were particularly liable to fall off (Ledger 1974, Mundy, Ledger, Friedman & Butchart 1989). This has also been found to be true for Cape Gannets *Sula capensis*, especially with black and white rings (Colclough & Ross 1987). Thus it is likely that some older birds will have lost all their colour rings and so will be less likely to be reported. This could lead to the estimate of adult survival being negatively biased.

Year to year variations

Because the ringing effort and search effort have varied from one year to the next, it is expected that there should be much variation in reporting rate with time. This is investigated in two ways. Firstly the logit of the reporting rate is estimated as a function of calendar year, where time is entered as a 'factor' variable, i.e. each year is a separate factor. Secondly, the reporting rate is regressed against a polynomial of time. Time, i.e. year, may be considered as a factor with 39 levels representing the years from 1948 to 1987, both years included, but 1949 excluded as no birds were ringed that year.

Component	*N*	*GLM Estimate*	*s.e.*	*t*	*Prob.*	*Reporting rate*
Constant	178	-3.40	1.02	-3.35	**0.05%**	3.2%
1950	2	-1.08	1.43	-0.75	22.7%	1.1%
1951	2	-6.18	8.33	-0.74	23.0%	0.01%
1952	2	-6.7	11.1	-0.61	27.1%	0.00%
1953	2	-0.73	1.24	-0.59	27.8%	1.5%
1954	2	-0.32	1.17	-0.27	39.3%	2.3%
1955	3	0.58	1.12	0.52	30.2%	5.6%
1956	2	-0.48	1.17	-0.41	34.1%	2.0%
1957	5	-0.82	1.13	-0.72	23.6%	1.4%
1958	3	-0.52	1.17	-0.45	32.6%	1.9%
1959	4	-0.06	1.14	-0.05	48.0%	3.0%
1960	4	-0.28	1.10	-0.25	40.1%	2.4%
1961	4	-1.70	1.43	-1.19	11.8%	0.6%
1962	4	-0.48	1.14	-0.42	33.8%	2.0%
1963	6	-0.83	1.13	-0.73	23.3%	1.4%
1964	4	-0.35	1.10	-0.32	37.5%	2.3%
1965	2	-0.25	1.17	-0.22	41.3%	2.5%
1966	3	0.61	1.08	0.56	28.8%	5.7%
1967	5	0.29	1.09	0.27	39.4%	4.2%
1968	4	-0.15	1.17	-0.13	44.8%	2.7%
1969	2	-0.64	1.24	-0.52	30.1%	1.7%
1970	3	-0.39	1.14	-0.35	36.3%	2.2%
1971	2	0.17	1.11	0.16	43.7%	3.8%
1972	3	0.02	1.25	0.01	49.7%	3.2%
1973	8	0.23	1.07	0.22	41.3%	4.0%
1974	7	0.65	1.05	0.62	26.9%	6.0%
1975	10	0.45	1.04	0.43	33.4%	4.9%
1976	10	0.87	1.03	0.84	20.1%	7.3%
1977	7	0.61	1.04	0.59	27.8%	5.7%
1978	7	0.70	1.04	0.67	25.2%	6.3%
1979	10	0.39	1.05	0.38	35.2%	4.7%
1980	8	0.25	1.06	0.24	40.5%	4.1%
1981	9	0.28	1.05	0.26	39.8%	4.2%
1982	9	0.58	1.04	0.56	28.8%	5.6%
1983	11	0.04	1.07	0.04	48.4%	3.3%
1984	2	2.01	1.29	1.56	6.0%	19.9%
1985	2	1.00	1.46	0.69	24.6%	8.3%
1986	2	0.84	1.45	0.58	28.1%	7.1%
1987	2	-5.0	13.9	-0.36	35.9%	0.0%

(Statistically significant coefficients are shown in bold.)

The deviance of the residuals is 146.6 with 139 degrees of freedom (mean deviance = 1.054) and the associated probability value (assuming asymptotic chi-square) is 32.3%, an adequate goodness-of-fit. There are 16 points with high leverage (i.e. Nos. 2, 4, 15, 16, 18, 20, 31, 32, 51, 52, 64, 66, 132, 138, 157 and 159 - see Table 5.9) and all these are from observations with a high number of birds ringed fairly early in the proceedings, with the exception of Nos. 132 and 138 from Potberg. There are two points which have high residuals (i.e. Nos. 4 and 69 - see Table 5.9). Observation No. 4 has no recoveries from 78 ringed (too low) and No. 69 has two recoveries from 4 - too high.

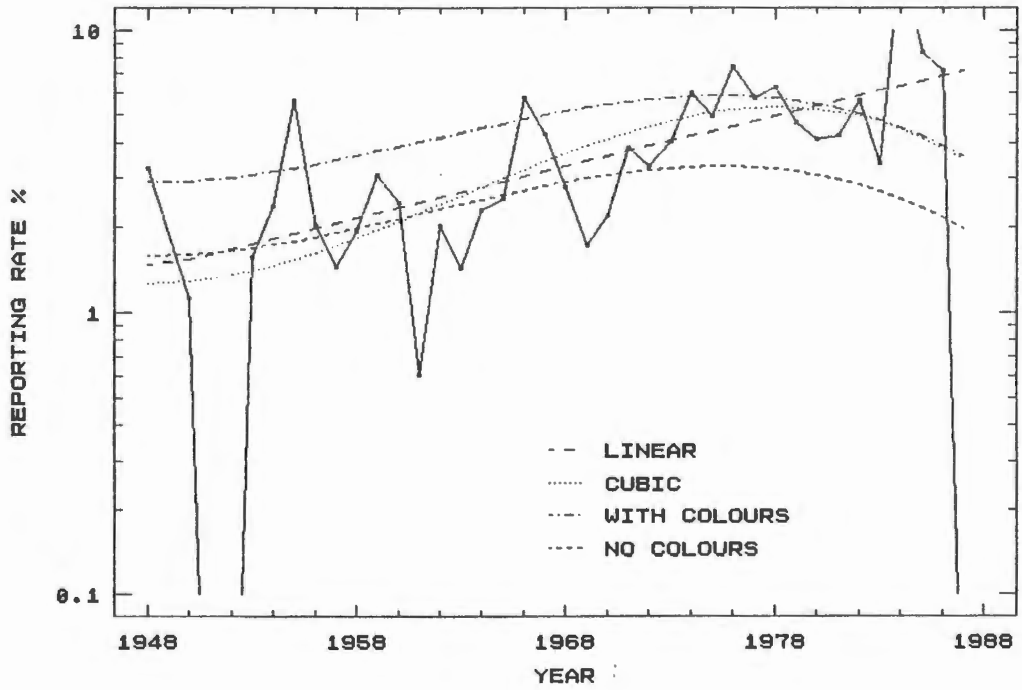

Figure 5.4 Variation in reporting rate as a function of time.

From an inspection of the reporting rate as a function of time (Figure 5.4) or the logit of the reporting rate as a function of time (Figure 5.5) it may be concluded that there may be a linear (or higher order) trend with time. To test this a GLM with time as a linear variable was constructed.

Component	*N*	*GLM Estimate*	*s.e.*	*t*	*Prob.*
Constant	178	-4.244	0.192	-22.07	**0.00%**
Year	178	0.04320	0.00721	5.99	**0.00%**

(Statistically significant coefficients are shown in bold.)

The deviance of the residuals is 190.5 with 176 degrees of freedom (mean deviance = 1.082) and the associated probability value (assuming asymptotic chi-square) is 21.5%, an adequate goodness-of-fit. There are 16 points with high leverage (i.e. Nos. 4, 13, 15, 16, 18, 19, 20, 32, 51, 80, 155, 156, 168, 171, 174 and 176 - see Table 5.9), the first nine observations with high leverage come from the early years while the remaining seven points come from the latter years; all have high numbers ringed. The early years have lower reporting rates than the later years, though none is statistically significant on its own (see previous analysis and Figures 5.4 and 5).

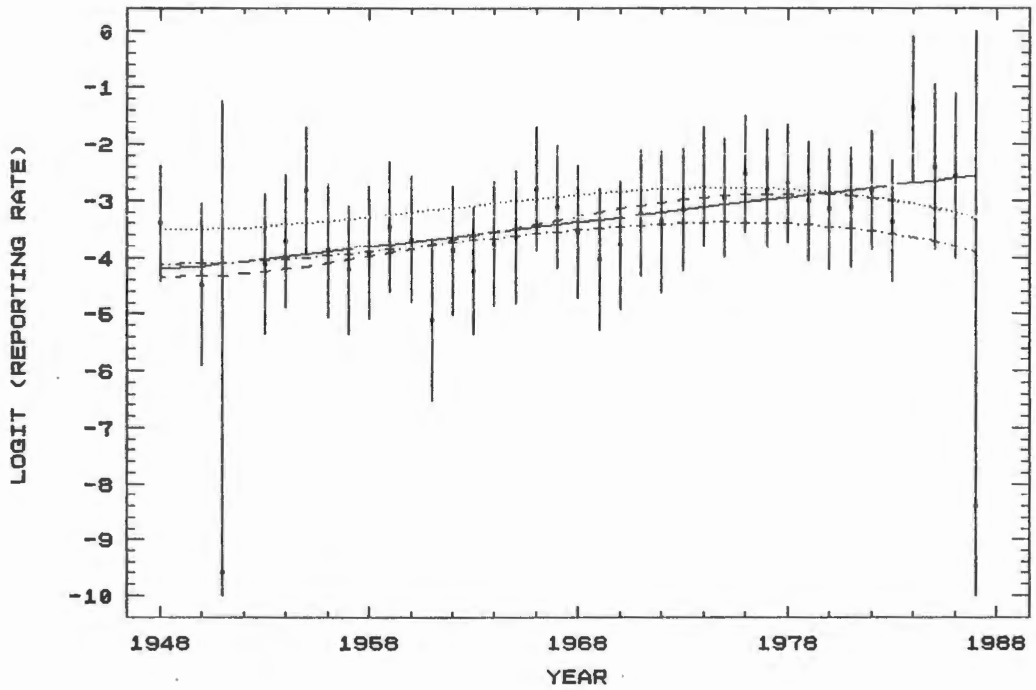

Figure 5.5 Variation in logit transform of the reporting rate as a function of time.

From an inspection of the linear GLM it seems as though there may be a higher-order component to the trend (Figures 5.4 and 5). To test this GLMs were constructed for all six combinations of year, year^2 and year^3. The most parsimonious model was chosen:

Component	*N*	*GLM Estimate*	*s.e.*	*t*	*Prob.*
Constant	178	-4.357	0.222	-19.66	**0.00%**
Year^2	178	0.00487	0.00121	4.02	**0.00%**
Year^3	178	-0.0001075	0.0000326	-3.30	**0.001%**

(Statistically significant coefficients are shown in bold.)

The deviance of the residuals is 184.2 with 175 degrees of freedom (mean deviance = 1.053) and the associated probability value (assuming asymptotic chi-square) is 30.2%, an adequate goodness-of-fit. There are 14 points with high leverage (i.e. Nos. 4, 15, 16, 18, 19, 32, 112, 155, 156, 163, 165, 168, 176 and 177 - see Table 5.9), the first six high-leverage points (i.e. 4, 15, .. 32) are from the earliest years and the last eight (i.e. Nos. 112, 155, ... 177) are from the latter years; all have large numbers of nestlings ringed. This cubic model indicates that there is a decline in reporting rate in the last decade of ringing (Figures 5.4 and 5) and this suggests that the reporting of rings may not yet be complete.

Table 5.9
Summary of recovery data for estimating reporting rate.

Line	Locality	Yrs	Rpx	Pfx	Aly	Clny	Afr	Yr	Col	No.	A	B	C
1	Roberts' Farm	50	B	1	1	10	0	2	1	11	0	1	0
2	Kranzberg	48	C	2	1	4	0	1	1	31	0	1	0
3	Potberg	51	C	2	1	9	0	3	1	2	0	0	0
4	Roberts' Farm	50	C	2	1	10	0	2	1	78	3	0	0
5	Skeerpoort	57	C	2	1	11	0	9	1	17	0	0	0
6	Skeerpoort	61	C	2	1	11	0	13	1	46	0	0	0
7	Kranzberg	52	508	3	1	4	0	4	1	14	0	0	0
8	Kranzberg	57	508	3	1	4	0	9	1	10	0	1	0
9	Mannyelanong	63	508	3	1	5	1	15	1	1	0	0	0
10	Mannyelanong	64	508	3	1	5	1	16	1	5	1	0	0
11	Potberg	59	508	3	1	9	0	11	1	1	0	0	0
12	Potberg	60	508	3	1	9	0	12	1	3	0	0	0
13	Roberts' Farm	51	508	3	1	10	0	3	1	76	2	0	0
14	Roberts' Farm	52	508	3	1	10	0	4	1	62	0	0	0
15	Roberts' Farm	53	508	3	1	10	0	5	1	119	1	2	0
16	Roberts' Farm	54	508	3	1	10	0	6	1	97	1	3	0
17	Roberts' Farm	55	508	3	1	10	0	7	1	36	0	2	0
18	Roberts' Farm	56	508	3	1	10	0	8	1	109	1	0	1
19	Roberts' Farm	57	508	3	1	10	0	9	1	161	3	1	0
20	Roberts' Farm	58	508	3	1	10	0	10	1	111	1	1	1
21	Roberts' Farm	59	508	3	1	10	0	11	1	42	0	0	0
22	Roberts' Farm	60	508	3	1	10	0	12	1	52	0	0	1
23	Roberts' Farm	61	508	3	1	10	0	13	1	34	0	1	0
24	Roberts' Farm	62	508	3	1	10	0	14	1	51	1	2	0
25	Skeerpoort	53	508	3	1	11	0	5	1	8	0	0	0
26	Skeerpoort	54	508	3	1	11	0	6	1	30	0	0	0
27	Skeerpoort	55	508	3	1	11	0	7	1	12	1	1	0
28	Skeerpoort	56	508	3	1	11	0	8	1	39	0	2	0
29	Skeerpoort	57	508	3	1	11	0	9	1	19	0	1	0
30	Skeerpoort	58	508	3	1	11	0	10	1	34	0	1	0
31	Skeerpoort	59	508	3	1	11	0	11	1	80	0	4	0
32	Skeerpoort	60	508	3	1	11	0	12	1	177	7	4	0
33	Skeerpoort	62	508	3	1	11	0	14	1	29	1	1	0
34	Skeerpoort	63	508	3	1	11	0	15	1	100	0	0	0
35	Skeerpoort	67	508	3	1	11	0	19	1	7	0	0	0
36	Skeerpoort	68	508	3	1	11	0	20	1	2	0	0	0
37	Mannyelanong	63	509	4	1	5	1	15	1	87	4	4	0
38	Mannyelanong	64	509	4	1	5	1	16	1	59	1	0	0
39	Nooitgedacht	62	509	4	1	8	0	14	1	33	0	1	0
40	Nooitgedacht	63	509	4	1	8	0	15	1	22	0	0	0
41	Potberg	65	509	4	1	9	0	17	1	6	0	0	0
42	Roberts' Farm	55	509	4	1	10	0	7	1	41	0	1	1
43	Roberts' Farm	58	509	4	1	10	0	10	1	10	0	0	0
44	Roberts' Farm	59	509	4	1	10	0	11	1	8	0	0	0
45	Roberts' Farm	60	509	4	1	10	0	12	1	11	0	1	0
46	Roberts' Farm	61	509	4	1	10	0	13	1	17	0	0	0
47	Roberts' Farm	63	509	4	1	10	0	15	1	49	2	0	0
48	Roberts' Farm	64	509	4	1	10	0	16	1	37	1	1	1
49	Skeerpoort	57	509	4	1	11	0	9	1	69	0	1	0
50	Skeerpoort	62	509	4	1	11	0	14	1	85	0	0	0

Table 5.9 (continued)

Line	Locality	Yrs	Rpx	Pfx	Aly	Clny	Afr	Yr	Col	No.	A	B	C
51	Skeerpoort	64	509	4	1	11	0	16	1	161	2	2	2
52	Skeerpoort	65	509	4	1	11	0	17	1	113	1	2	1
53	Skeerpoort	66	509	4	1	11	0	18	1	11	0	1	0
54	Skeerpoort	67	509	4	1	11	0	19	1	72	2	2	1
55	Skeerpoort	68	509	4	1	11	0	20	1	2	1	0	0
56	Skeerpoort	70	509	4	1	11	0	22	1	93	3	2	2
57	Skeerpoort	61	546	5	1	11	0	13	1	69	0	0	0
58	Skeerpoort	63	546	5	1	11	0	15	1	20	0	0	0
59	Skeerpoort	68	546	5	1	11	0	20	1	4	1	0	0
60	Skeerpoort	69	546	5	1	11	0	21	1	34	0	0	0
61	Mannyelanong	67	658	6	1	5	1	19	1	10	0	1	0
62	Roberts' Farm	66	658	6	1	10	0	18	1	6	0	0	0
63	Roberts' Farm	67	658	6	1	10	0	19	1	38	0	0	0
64	Skeerpoort	66	658	6	1	11	0	18	1	122	1	6	1
65	Skeerpoort	67	658	6	1	11	0	19	1	37	0	1	2
66	Skeerpoort	68	658	6	1	11	0	20	1	100	3	2	1
67	Aasvogelvlei	81	G	7	0	1	0	33	2	6	1	0	0
68	Aasvogelvlei	82	G	7	0	1	0	34	2	5	0	0	0
69	Aasvogelvlei	83	G	7	0	1	0	35	2	4	0	0	2
70	Aasvogelvlei	84	G	7	0	1	0	36	2	4	1	0	0
71	Aasvogelvlei	85	G	7	0	1	0	37	2	6	0	0	0
72	Aasvogelvlei	86	G	7	0	1	0	38	2	8	0	0	1
73	Aasvogelvlei	87	G	7	0	1	0	39	2	4	0	0	0
74	Colleywobbles	76	G	7	0	2	1	28	2	40	1	3	0
75	Colleywobbles	77	G	7	0	2	1	29	2	18	0	1	0
76	Colleywobbles	78	G	7	0	2	1	30	2	70	2	3	0
77	Colleywobbles	79	G	7	0	2	1	31	2	57	1	3	0
78	Colleywobbles	80	G	7	0	2	1	32	1	1	0	0	0
79	Colleywobbles	80	G	7	0	2	1	32	2	33	0	3	0
80	Colleywobbles	81	G	7	0	2	1	33	2	92	3	2	1
81	Colleywobbles	82	G	7	0	2	1	34	2	57	0	6	1
82	Colleywobbles	83	G	7	0	2	1	35	1	1	0	0	0
83	Colleywobbles	83	G	7	0	2	1	35	2	38	0	2	0
84	Karnmelkspruit	80	G	7	0	3	0	32	2	17	0	0	0
85	Mannyelanong	73	G	7	0	5	1	25	1	1	0	0	0
86	Mannyelanong	73	G	7	0	5	1	25	2	1	0	0	0
87	Mannyelanong	74	G	7	0	5	1	26	2	27	1	1	0
88	Mannyelanong	75	G	7	0	5	1	27	1	1	0	0	0
89	Mannyelanong	75	G	7	0	5	1	27	2	53	7	2	1
90	Mannyelanong	76	G	7	0	5	1	28	1	2	0	0	0
91	Mannyelanong	76	G	7	0	5	1	28	2	59	2	1	4
92	Mannyelanong	77	G	7	0	5	1	29	2	55	6	1	0
93	Mannyelanong	78	G	7	0	5	1	30	2	52	2	2	0
94	Mannyelanong	79	G	7	0	5	1	31	1	4	0	0	1
95	Mannyelanong	79	G	7	0	5	1	31	2	47	5	0	1
96	Mannyelanong	80	G	7	0	5	1	32	2	27	2	0	1
97	Mannyelanong	81	G	7	0	5	1	33	1	1	0	0	0
98	Mannyelanong	81	G	7	0	5	1	33	2	37	0	1	0
99	Mannyelanong	82	G	7	0	5	1	34	2	39	3	0	0
100	Mannyelanong	83	G	7	0	5	1	35	1	14	2	0	0

Table 5.9 (continued)

Line	Locality	Yrs	Rpx	Pfx	Aly	Clny	Afr	Yr	Col	No.	A	B	C
101	Mannyelanong	83	G	7	0	5	1	35	2	9	2	0	2
102	Manoutsa	75	G	7	0	6	0	27	2	14	0	0	0
103	Manoutsa	76	G	7	0	6	0	28	1	1	0	0	0
104	Manoutsa	76	G	7	0	6	0	28	2	34	0	0	0
105	Manoutsa	77	G	7	0	6	0	29	2	24	1	1	0
106	Manoutsa	78	G	7	0	6	0	30	2	32	1	1	0
107	Manoutsa	79	G	7	0	6	0	31	1	1	0	0	0
108	Manoutsa	79	G	7	0	6	0	31	2	52	0	1	0
109	Manoutsa	80	G	7	0	6	0	32	2	48	0	0	1
110	Manoutsa	81	G	7	0	6	0	33	2	46	0	0	0
111	Manoutsa	82	G	7	0	6	0	34	2	64	0	1	1
112	Manoutsa	83	G	7	0	6	0	35	1	47	0	1	0
113	Manyana	73	G	7	0	7	1	25	1	6	0	0	0
114	Manyana	73	G	7	0	7	1	25	2	15	2	0	0
115	Manyana	74	G	7	0	7	1	26	2	13	1	1	0
116	Manyana	75	G	7	0	7	1	27	1	1	0	0	0
117	Manyana	75	G	7	0	7	1	27	2	12	2	0	0
118	Manyana	76	G	7	0	7	1	28	2	5	3	0	1
119	Manyana	83	G	7	0	7	1	35	2	1	0	0	0
120	Potberg	72	G	7	0	9	0	24	1	14	1	0	0
121	Potberg	73	G	7	0	9	0	25	1	14	1	0	1
122	Potberg	74	G	7	0	9	0	26	2	22	0	1	1
123	Potberg	75	G	7	0	9	0	27	2	15	2	1	0
124	Potberg	76	G	7	0	9	0	28	2	11	3	0	0
125	Potberg	77	G	7	0	9	0	29	2	13	1	1	2
126	Potberg	78	G	7	0	9	0	30	2	7	0	0	0
127	Potberg	79	G	7	0	9	0	31	2	9	1	0	0
128	Potberg	80	G	7	0	9	0	32	2	6	0	0	0
129	Potberg	81	G	7	0	9	0	33	2	7	1	0	1
130	Potberg	82	G	7	0	9	0	34	2	10	5	0	1
131	Potberg	83	G	7	0	9	0	35	2	5	0	0	0
132	Potberg	84	G	7	0	9	0	36	2	6	0	0	2
133	Potberg	85	G	7	0	9	0	37	2	6	0	0	1
134	Potberg	86	G	7	0	9	0	38	2	6	0	0	0
135	Potberg	87	G	7	0	9	0	39	2	5	0	0	0
136	Roberts' Farm	70	G	7	0	10	0	22	1	29	0	0	0
137	Roberts' Farm	71	G	7	0	10	0	23	1	30	0	2	1
138	Roberts' Farm	72	G	7	0	10	0	24	1	40	4	1	1
139	Roberts' Farm	73	G	7	0	10	0	25	1	51	7	1	1
140	Roberts' Farm	73	G	7	0	10	0	25	2	54	6	0	3
141	Roberts' Farm	74	G	7	0	10	0	26	1	3	2	0	0
142	Roberts' Farm	74	G	7	0	10	0	26	2	102	17	3	2
143	Roberts' Farm	75	G	7	0	10	0	27	1	6	0	0	0
144	Roberts' Farm	75	G	7	0	10	0	27	2	126	27	3	5
145	Roberts' Farm	76	G	7	0	10	0	28	2	110	10	10	0
146	Roberts' Farm	77	G	7	0	10	0	29	1	18	0	2	0
147	Roberts' Farm	77	G	7	0	10	0	29	2	80	19	4	1
148	Roberts' Farm	78	G	7	0	10	0	30	1	3	0	0	0
149	Roberts' Farm	78	G	7	0	10	0	30	2	63	8	5	1
150	Roberts' Farm	79	G	7	0	10	0	31	1	6	0	0	0

Table 5.9 (continued)

Line	Locality	Yrs	Rpx	Pfx	Aly	Clny	Afr	Yr	Col	No.	A	B	C
151	Roberts' Farm	79	G	7	0	10	0	31	2	60	2	5	2
152	Roberts' Farm	80	G	7	0	10	0	32	2	73	6	3	1
153	Roberts' Farm	81	G	7	0	10	0	33	2	51	6	2	1
154	Roberts' Farm	82	G	7	0	10	0	34	1	4	0	0	0
155	Roberts' Farm	82	G	7	0	10	0	34	2	86	4	3	2
156	Roberts' Farm	83	G	7	0	10	0	35	1	111	0	2	0
157	Skeerpoort	69	G	7	0	11	0	21	1	82	2	2	0
158	Skeerpoort	70	G	7	0	11	0	22	1	60	0	0	0
159	Skeerpoort	71	G	7	0	11	0	23	1	101	1	2	0
160	Skeerpoort	72	G	7	0	11	0	24	1	7	0	0	0
161	Skeerpoort	73	G	7	0	11	0	25	1	81	1	3	0
162	Skeerpoort	74	G	7	0	11	0	26	1	3	0	0	0
163	Skeerpoort	74	G	7	0	11	0	26	2	130	5	6	3
164	Skeerpoort	75	G	7	0	11	0	27	1	3	0	0	0
165	Skeerpoort	75	G	7	0	11	0	27	2	133	12	4	2
166	Skeerpoort	76	G	7	0	11	0	28	1	2	0	0	0
167	Skeerpoort	76	G	7	0	11	0	28	2	128	16	9	1
168	Skeerpoort	77	G	7	0	11	0	29	2	155	15	7	1
169	Skeerpoort	78	G	7	0	11	0	30	2	107	9	4	5
170	Skeerpoort	79	G	7	0	11	0	31	1	3	0	0	0
171	Skeerpoort	79	G	7	0	11	0	31	2	122	4	4	0
172	Skeerpoort	80	G	7	0	11	0	32	2	62	3	0	2
173	Skeerpoort	81	G	7	0	11	0	33	1	2	0	0	0
174	Skeerpoort	81	G	7	0	11	0	33	2	90	2	3	3
175	Skeerpoort	82	G	7	0	11	0	34	1	2	0	0	0
176	Skeerpoort	82	G	7	0	11	0	34	2	89	2	2	3
177	Skeerpoort	83	G	7	0	11	0	35	1	48	1	1	0
178	Skeerpoort	83	G	7	0	11	0	35	2	20	0	0	0
								Total		7130	302	190	83

Column headings:

Year = Calender year
Rpx = Ring prefix
Pfx = Numeric code for ring prefix, 1='B', 2='C' etc.
Aly = Type of metal, 0=Monel and 1=Aluminium
Clny = Numeric code for colony, 1=Aasvogelvlei etc.
Afr = 0=Not in African subsistence farming region, 1=Yes
Yr = Year-1947 = year relative to 1948.
Col = Colour rings fitted 1=Metal ring only, 2=Colour rings fitted
No. = Number of nestlings ringed
A = Number of recoveries of nestlings and indeterminates
B = Number found dead at natal colony, definitely fledged
C = Number found dead away from the colony

Summary and final model

In the analyses presented above five different comparisons were drawn. From each univariate analysis the following conclusions may be made, though it must be borne in mind that the analyses overlap (e.g. the comparison of reporting rates of colonies from subsistence farming areas with those from commercial farming areas overlaps with the comparisons between colonies).

1) Of the ring prefixes, 'C' has a much lower reporting rate, 'B' had a much higher reporting rate and the use of ring prefix provides an adequate model.
2) Monel rings have twice the reporting rate of aluminium rings. This may be because aluminium rings are lost more easily or because monel rings were also fitted with colour rings and this may have enhanced the reporting rate. The use of ring type provides an adequate model.
3) The reporting rate from Manoutsa is significantly lower than that from other colonies while the reporting rate of recoveries from Aasvogelvlei is significantly higher. Colony is not an adequate explanatory variable for reporting rate.
4) The use of colour rings doubles the reporting rate and is an adequate explanatory variable on its own.
5) No one year on its own yields a significantly lower or higher reporting rate, though reporting rate may be adequately modelled by both linear and quadratic trends.

To find the most parsimonious model a series of multivariate GLMs were evaluated. Of these an adequate and simple model was chosen:

Component	*N*	*GLM Estimate*	*s.e.*	*t*	*Prob.*
Constant	178	-4.121	0.227	-18.18	**0.0%**
$Year^2$	178	0.00297	0.00137	2.17	**1.6%**
$Year^3$	178	-0.0000724	0.0000348	-2.08	**1.9%**
Colour ringed	74	0.605	0.217	2.79	**0.3%**

(Statistically significant coefficients are shown in bold.)

The deviance of the residuals is 175.6 with 174 degrees of freedom (mean deviance = 1.009) and the associated probability value (assuming asymptotic chi-square) is 45.2%, an adequate goodness-of-fit. There are 14 points with high leverage (i.e. Nos. 15, 19, 56, 112, 142, 144, 155, 156, 159, 161, 163, 165, 176 and 177 - see Table 5.9), the first three high-leverage points (i.e. 15, 19 and 56) are from the earliest years and the last 11 (i.e. Nos. 112, 142, ... 177) are from the latter years; all have large numbers of nestlings ringed. This final model incorporates a cubic response with respect to time (i.e. calendar year of ringing) which reaches a maximum of about 3¼% of ringed birds being reported as significant recoveries in about 1976, if they have not been colour-ringed and nearly 6% if they carry colour rings (Figures 5.4 and .5). The final decline may indicate that the recovery-reporting process is not yet complete.

5.2.3 Survival estimates from ringing-recovery data

When these researches were undertaken it was believed that it was impossible to estimate age-specific survival from ring-recovery data given that all birds were ringed as nestlings (Brownie, Anderson, Burnham & Robson 1985: 112):

> *We cannot emphasize too strongly that, based on our current knowledge, there is no valid way to estimate age-specific survival rates from only the banding of young.*

However, this is no longer the case. The recent models developed by BTJ Morgan and his student SN Freeman may have overcome many of these dificulties (Freeman & Morgan 1990, 1992; Morgan & Freeman 1989; BTJ Morgan, pers. comm.). Not having access to these latest tools only the simplest analysis of the Cape Vulture ring-recovery data will be undertaken. If it is assumed that survival is a function of age only, invariant of time and if the reporting rate is constant for all age-classes and for the whole study period then it is possible to provide estimates of age-specific survival (Seber 1982: 252). This analysis is undertaken in order to compare the estimates using the 295[1] significant recoveries (Table 5.10; Figure 5.6) with those of Piper, Mundy & Ledger (1981)[2] which used 118. The 'confidence limits' are based on the assumption that the number of survivors in each class are known exactly, whereas this is not the case and the limits are provided for the purpose of comparison only. If birds start to breed in their sixth year (see Chapter Four) then the number surviving past the fifth year constitute the 'recruitment' to the adult population.

The most interesting feature of these results is the higher first year survival rate, about two and a half times that of Piper, Mundy & Ledger (1981). This cannot be a reflection of an increased sample size because that would just narrow the confidence limits. Rather it is an indication of a change in recovery process with proportionately more adults having been reported, probably as a result of having switched from aluminium to monel rings at the start of the 1970s as well as the use of colour rings.

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[1] In the previous section a subset of 273 significant recoveries were used - nestlings ringed at a number of small colonies were excluded from the analysis - however, the full set is used here.

[2] The method of Piper, Mundy & Ledger (1981) is based on a maximum likelihood model but is not used here because of the criticism of Anderson, Burnham & White (1985)

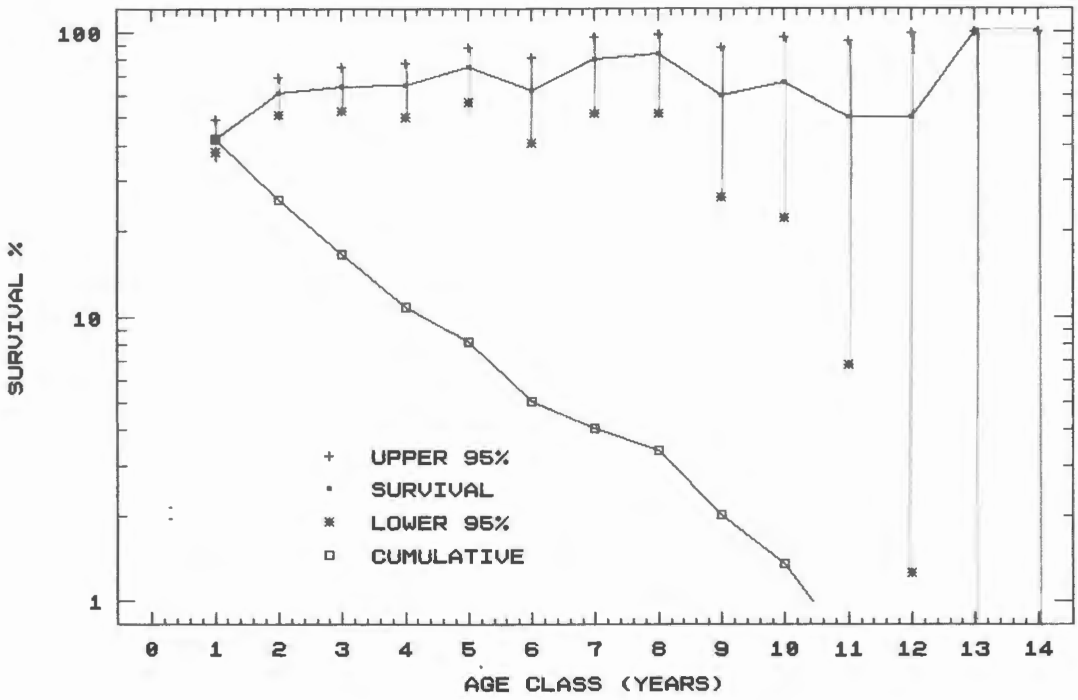

Figure 5.6 Estimates of age-specific survival rates with associated 95% confidence limits.

Table 5.10
Estimates of age-specific survival using all recovery data.
Based on the model in Seber (1982: 252) model, but see caveat in text.
(95% confidence limits based on the binomial distribution - Diem & Lentner 1970: 85ff.)

Age class	Start	Die	Live	Survive	Lower 95% limit	Upper 95% limit	Cumulative survival	
First	295	171	124	42.0%	37.7%	49.2%	42.0%	
Second	124	48	76	61.3%	51.5%	69.5%	25.8%	
Third	76	27	49	64.5%	52.7%	75.1%	16.6%	
Fourth	49	17	32	65.3%	50.4%	78.1%	10.9%	
Fifth	32	8	24	75.0%	56.6%	88.5%	8.1%	Recruitment
Sixth	24	9	15	62.5%	40.6%	81.2%	5.1%	
Seventh	15	3	12	80.0%	51.9%	95.7%	4.1%	
Eighth	12	2	10	83.3%	51.6%	97.9%	3.4%	
Ninth	10	4	6	60.0%	26.2%	87.8%	2.0%	
Tenth	6	2	4	66.7%	22.3%	95.7%	1.4%	
Eleventh	4	2	2	50.0%	6.8%	93.2%	.7%	
Twelfth	2	1	1	50.0%	1.3%	98.7%	.3%	
Thirteenth	1	0	1	100.0%	0.0%	100.0%	.3%	
Fourteenth	1	1	0	.0%	0.0%	100.0%	.0%	

5.2.4 Survival estimates from ringing-resighting data

The most serious problem encountered when estimating survival from recoveries is the need to model the rate at which dead, ringed birds are reported (see section 5.2.2 above). An alternative to estimating survival from recoveries is to use observations of uniquely marked birds, i.e. resightings; in this way survival may be monitored directly. Observations of colour-ringed Cape Vultures in the south-western Cape are to be used for this purpose. This sub-population is particularly suitable for the reasons listed below.

1) The population, based at Potberg, Aasvogelvlei and a few other sites north of Bredasdorp, is functionally isolated from the rest of the Cape Vulture population in southern Africa, i.e. there is almost no immigration into, or emigration from the region (Boshoff & Vernon 1980).
2) The population has been declining very slowly over the last forty years and although it is not exactly constant, it is almost so, especially from the mid 1970's (Boshoff & Robertson 1985; Boshoff & Scott 1990; see also section 3.3).
3) From 1974 until 1988 nearly all the nestlings raised at Potberg and Aasvogelvlei were fitted with a unique permutation of colour rings, as well as the standard numbered metal (monel) ring.
4) While irregular observations were made of marked birds from 1974 onwards, consistent and regular observations were made at the main breeding sites, roosts and at carcasses from 1980 when a study of breeding biology commenced (Robertson 1984). Following this, observations were continued by members of the Cape Department of Nature and Environmental Conservation (CDNEC). After a conservation plan was drawn up (Boshoff & Robertson 1985: 30) regular observations were made part of the work-plan of the local CDNEC technician (loc. cit.; A. Scott *pers. comm.*).

A complete set of the ringing, resighting and recovery data has been collated for the south-western Cape (CDNEC - details in Piper, Mundy & Mundy, in prep.) from which a summary of the years in which each colour-marked bird was ringed and last seen was compiled for the period 1978 to 1990, both years inclusive (Table 5.11)[1]. From this summary an abstract has been constructed (Table 5.12) giving the number of birds, in each age-class, alive at the start of each calendar year as well as the number of them which survive until the start of the next calendar year.

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[1] The numbers of nestlings used to track survival in these analyses are less than the totals shown for the southwestern Cape in section 5.2.1 above by one for each of the years 1982, 1985, 1986 and 1987 because free-flying birds caught and ringed are excluded. Such birds were found sick or injured and ringed once that had been rehabilitated and returned to the wild. Often their age at release was not known.

Table 5.11
History of each colour-ringed nestling Cape Vulture in the south-western Cape.
(A '1' in a column indicates that the bird was alive at the year-end. The last observations recorded are from April and May, 1990)

RING	COLOUR	YEAR	last	'79	'80	'81	'82	'83	'84	'85	'86	'87	'88	'89
G09008	GBG- MB	1979	1979	1	0	0	0	0	0	0				
G09382	BYB- MB	1979	1979	1	0	0	0	0	0	0				
G09387	YGB- MB	1979	1979	1	0	0	0	0	0	0				
G09004	RWG- MB	1979	1979	1	0	0	0	0	0	0				
G09377	BWB- MB	1979	1979	1	0	0	0	0	0	0				
G09335	YGY- MB	1979	1979	1	0	0	0	0	0	0				
G09385	WGB- MB	1979	1980	1	0	0	0	0	0	0				
G09371	RYG- MB	1979	1982	1	1	1	0	0	0	0				
G08973	WRB- MB	1979	1985	1	1	1	1	1	1	0				
			Summary	**9**	**2**	**2**	**1**	**1**	**1**	**0**				
G09374	GRB- MB	1980	1980		1	0	0	0	0	0	0	0	0	
G09396	BYW- MB	1980	1980		1	0	0	0	0	0	0	0	0	
G09391	WSB- MB	1980	1980		1	0	0	0	0	0	0	0	0	
G09373	YRB- MB	1980	1981		1	0	0	0	0	0	0	0	0	
G09390	YSR- MB	1980	1985		1	1	1	1	1	0	0	0	0	
G09392	GSB- MB	1980	1989		1	1	1	1	1	1	1	1	1	
				Summary	**6**	**2**	**2**	**2**	**2**	**1**	**1**	**1**	**1**	
G09410	YSB-MWB	1981	1981			1	0	0	0	0	0	0	0	
G13854	MWB-BYG	1981	1981			1	0	0	0	0	0	0	0	
G09375	RSB-MWB	1981	1982			1	0	0	0	0	0	0	0	
G09397	RYW-MWB	1981	1982			1	0	0	0	0	0	0	0	
G09407	GBW-MWB	1981	1982			1	0	0	0	0	0	0	0	
G13842	MWB-WYR	1981	1982			1	0	0	0	0	0	0	0	
G13827	MWB-RWG	1981	1982			1	0	0	0	0	0	0	0	
G13839	MWB-YBR	1981	1984			1	1	1	0	0	0	0	0	
G13836	MWB-RWR	1981	1985			1	1	1	1	0	0	0	0	
G13835	MWB-YWR	1981	1985			1	1	1	1	0	0	0	0	
G13824	MWB-GSR	1981	1987			1	1	1	1	1	1	0	0	
G09418	YSW-MWB	1981	1987			1	1	1	1	1	1	0	0	
G13845	MWB-GYR	1981	1987			1	1	1	1	1	1	0	0	
					Summary	**13**	**6**	**6**	**5**	**3**	**3**	**0**	**0**	
G13880	MB-YGY	1982	1982				1	0	0	0	0	0	0	0
G13844	MWB-RYR	1982	1982				1	0	0	0	0	0	0	0
G13867	MB-YWY	1982	1982				1	0	0	0	0	0	0	0
G13859	MB-YRG	1982	1982				1	0	0	0	0	0	0	0
G13838	MWB-RBG	1982	1982				1	0	0	0	0	0	0	0
G13825	MWB-YBG	1982	1982				1	0	0	0	0	0	0	0
G13840	MWB-WYG	1982	1983				1	0	0	0	0	0	0	0
G13874	MB-WRY	1982	1983				1	0	0	0	0	0	0	0
G13843	MWB-BYR	1982	1986				1	1	1	1	0	0	0	0
G13821	MWB-BWG	1982	1986				1	1	1	1	0	0	0	0
G13830	MWB-BSR	1982	1987				1	1	1	1	1	0	0	0
G13851	MWB-WBR	1982	1987				1	1	1	1	1	0	0	0
G13878	MB-WGY	1982	1988				1	1	1	1	1	1	0	0
G13885	MB-RSY	1982	1989				1	1	1	1	1	1	1	0
G13850	MWB-WSR	1982	1990				1	1	1	1	1	1	1	1
						Summary	**15**	**7**	**7**	**7**	**5**	**3**	**2**	**1**

Table 5.11 (Continued)

RING	COLOUR	YEAR	last	'83	'84	'85	'86	'87	'88	'89	'90
G13849	MWB-RGR	1983	1983	1	0	0	0	0	0	0	0
G13879	MB-BGY	1983	1983	1	0	0	0	0	0	0	0
G13829	MWB-WBG	1983	1983	1	0	0	0	0	0	0	0
G13871	MB-YBY	1983	1985	1	1	0	0	0	0	0	0
G13858	MB-BRG	1983	1985	1	1	0	0	0	0	0	0
G13846	MWB-WGR	1983	1987	1	1	1	1	0	0	0	0
G13872	MB-RBY	1983	1990	1	1	1	1	1	1	1	0
G13884	MB-YSY	1983	1990	1	1	1	1	1	1	1	0
G13875	MB-BRY	1983	1990	1	1	1	1	1	1	1	0
			Summary	**9**	**6**	**4**	**4**	**3**	**3**	**3**	**0**
G13856	MWB-GYG	1984	1984		1	0	0	0	0	0	0
G13834	MWB-BWR	1984	1985		1	0	0	0	0	0	0
G13837	MWB-GWR	1984	1986		1	1	0	0	0	0	0
G13828	MWB-GWG	1984	1987		1	1	1	0	0	0	0
G13826	MWB-YWG	1984	1987		1	1	1	0	0	0	0
G13823	MWB-RSR	1984	1988		1	1	1	1	0	0	0
G13822	MWB-YSR	1984	1988		1	1	1	1	0	0	0
G13870	MWB-WBY	1984	1990		1	1	1	1	1	1	0
G13882	MWB-WSY	1984	1990		1	1	1	1	1	1	0
G13868	MWB-RWY	1984	1990		1	1	1	1	1	1	0
				Summary	**10**	**8**	**7**	**5**	**3**	**3**	**0**
G13881	MWB-RGY	1985	1986			1	0	0	0	0	0
G13873	MWB-GBY	1985	1986			1	0	0	0	0	0
G13862	MWB-BSG	1985	1987			1	1	0	0	0	0
G13863	MWB-YSG	1985	1987			1	1	0	0	0	0
G13866	MWB-YWB	1985	1987			1	1	0	0	0	0
G13861	MWB-WSG	1985	1988			1	1	1	0	0	0
G13865	MWB-GSG	1985	1988			1	1	1	0	0	0
G13864	MWB-RSG	1985	1988			1	1	1	0	0	0
G13841	MWB-GBR	1985	1988			1	1	1	0	0	0
G13857	MWB-WRG	1985	1990			1	1	1	1	1	0
G13886	MWB-GSY	1985	1990			1	1	1	1	1	0
G13877	MWB-GRY	1985	1990			1	1	1	1	1	0
					Summary	**12**	**10**	**7**	**3**	**3**	**0**
G13942	YBW-MWB	1986	1986				1	0	0	0	0
G13935	BRB- MB	1986	1986				1	0	0	0	0
G13944	WBW-MWB	1986	1987				1	0	0	0	0
G13860	MWB-GRG	1986	1987				1	0	0	0	0
G13931	MB-RYG	1986	1987				1	0	0	0	0
G13926	MB-GRG	1986	1987				1	0	0	0	0
G13853	MWB-RBR	1986	1987				1	0	0	0	0
G13928	MB-GYB	1986	1988				1	1	0	0	0
G13932	MB-RBR	1986	1989				1	1	1	0	0
G13933	MB-BSY	1986	1990				1	1	1	1	0
G13945	MB-WYW	1986	1990				1	1	1	1	0
G13855	MWB-RYB	1986	1990				1	1	1	1	0
G09372	MWB-BRB	1986	1990				1	1	1	1	0
G13943	RWB-MWB	1986	1990				1	1	1	1	0
						Summary	**14**	**7**	**6**	**5**	**0**

Table 5.11 (Continued)

RING	COLOUR	YEAR	last	'87	'88	'89	'90
G18066	MWB-BGW	1987	1987	1	0	0	0
G18071	MWB-GSW	1987	1988	1	0	0	0
G18059	RSW-MWB	1987	1988	1	0	0	0
G18058	BSW-MWB	1987	1988	1	0	0	0
G18061	MWB-GYW	1987	1988	1	0	0	0
G18064	MWB-GRW	1987	1988	1	0	0	0
G18062	MWB-BRW	1987	1989	1	1	0	0
G18073	MWB-GBW	1987	1990	1	1	1	0
G18068	MWB-RGW	1987	1990	1	1	1	0
			Summary	9	3	2	0

The simplest estimate of survival is a constant, i.e. independent of age and time. However such a simple estimate 'cannot be considered valid' (Houston 1974; see section 5.1). It is suspected that survival will be a function of both age (see section 5.2.3 above) and year (survival may vary from year to year in a manner analogous to the year to year variations observed in breeding; see Chapter Four).

Initially age-specific estimates of survival will be computed from these south-western Cape Vulture colour-ring resighting data. Then year-specific estimates of survival will be computed. It will be seen that the assumption that survival is a function of age-only or year-only is inadequate. Thereafter a model will be developed in which survival is estimated as a function of both age and year. It will be seen that this model provides an adequate account of the observations.

Age-specific survival: Independent estimates[2]

In this first model to be constructed it is assumed that survival is a function of age only and that the survival rate of any one age class is independent of all other age classes. In other words, it is not assumed that survival increases monotonically with age, or in any other such fashion.

Let S_i be the probability that an individual aged (i-1) years at the start of a calendar year will survive until the start of the next calendar year when it will be i years old. Given that there are N_i individuals, aged (i-1) years alive at the start of any given year and that n_i of these survive to be alive exactly a year later then the appropriate probability distribution for this is the binomial (see Burnham, Anderson, White, Brownie & Pollock 1987: 6 ff. who deal with the multinominal, of which the binomial is a special case). Furthermore, the age-specific survival rate, S_i may be estimated from the ratio n_i/N_i (Table 5.13). The survival rates of age-classes 2 onwards are approximately constant (Figure 5.7), this will be investigated further below.

---

[2] All the estimates produced in this section are minimum estimates of survival - a bird emigrating is counted as lost and hence dead even though it lives on unobserved.

Table 5.12

Summary of survival as a function of year and age.

Obs.	Year	Age	Start	Survive
1	1979	1	9	2
2	1980	2	2	2
3	1981	3	2	1
4	1982	4	1	1
5	1983	5	1	1
6	1984	6	1	0
7	1980	1	6	2
8	1981	2	2	2
9	1982	3	2	2
10	1983	4	2	2
11	1984	5	2	1
12	1985	6	1	1
13	1986	7	1	1
14	1987	8	1	1
15	1988	9	1	0
16	1981	1	13	6
17	1982	2	6	6
18	1983	3	6	5
19	1984	4	5	3
20	1985	5	3	3
21	1986	6	3	0
22	1982	1	15	7
23	1983	2	7	7
24	1984	3	7	7
25	1985	4	7	5
26	1986	5	5	3
27	1987	6	3	2
28	1988	7	2	1
29	1983	1	9	6
30	1984	2	6	4
31	1985	3	4	4
32	1986	4	4	3
33	1987	5	3	3
34	1988	6	3	3
35	1984	1	10	8
36	1985	2	8	7
37	1986	3	7	5
38	1987	4	5	3
39	1985	1	12	10
40	1986	2	10	7
41	1987	3	7	3
42	1988	4	3	3
43	1986	1	14	7
44	1987	2	7	6
45	1988	3	6	5
46	1987	1	9	3
47	1988	2	3	2

Table 5.13

Age-specific survival estimates from observations of colour-ringed Cape Vultures in the South-western Cape. (Approximate 95% confidence limits estimated from Diem & Lentner 1970: 85 ff.)

	Number at		Survival	95% Confidence limits	
Age	Start	End	rate	Lower	Upper
1	97	51	52.6%	42.2%	62.8%
2	51	43	84.3%	71.4%	93.0%
3	41	32	78.1%	62.4%	89.4%
4	27	20	74.1%	53.7%	88.8%
5	14	11	78.6%	49.2%	95.3%
6	11	6	54.6%	23.4%	83.3%
7	3	2	66.7%	9.4%	99.2%
8	1	1	100.0%	0.0%	100.0%
9	1	0	0.0%	0.0%	100.0%

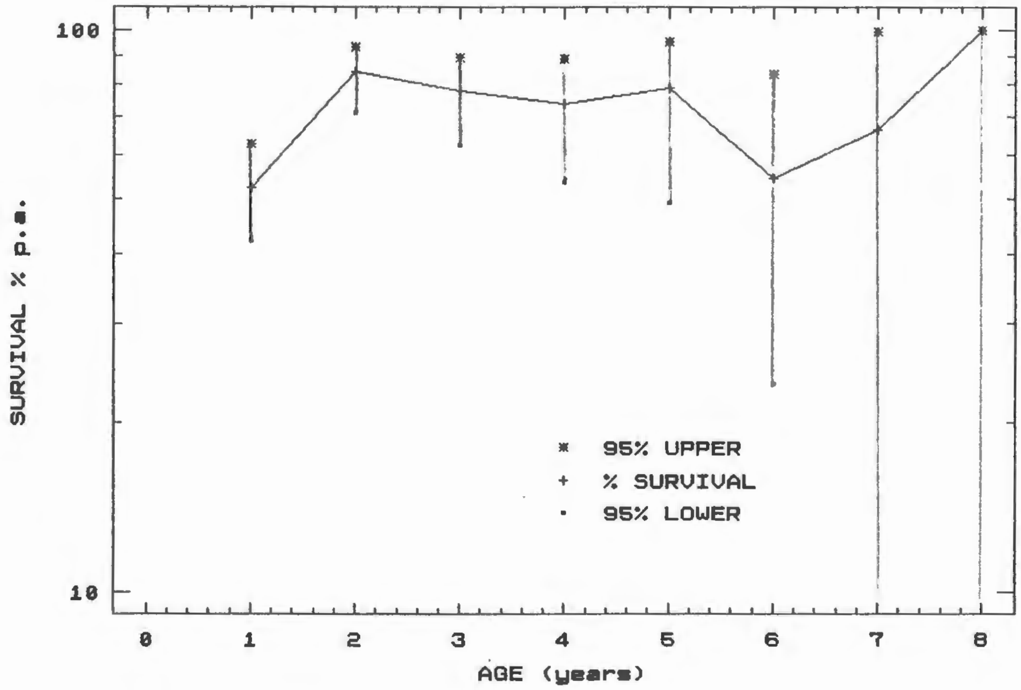

Figure 5.7 Estimates of survival as a function of age for colour-ringed birds in the southwestern Cape.

The survival rate may also be estimated using a generalized linear model (GLM). The response variable is modelled as a binomial and the logit transform is used as the link function (McCullach & Nelder 1989: 107 ff.). The logit transform for a binomial response is:

$\mathrm{Logit}(S_i) = \mathrm{Ln}(S_i/\{1\text{-}S_i\}) = \alpha_0 + F_i$ where F_i is the age-specific factor for the i^{th} age class.

The reverse transformation is:

$S_i = \exp(\alpha_0 + F_i)/\{1 + \exp(\alpha_0 + F_i)\}$

Fitting this GLM yields the same results as applying the binomial approximations directly (Table 5.13). The advantage of estimating model parameters by fitting a GLM is that a goodness-of-fit measure is provided, as well as indications of which data items are influential or outliers. Repeating the above analysis by fitting a GLM yields the results shown on the next page. The deviance of the residuals is 57.7 with 38 degrees of freedom (mean deviance = 1.519) and the associated probability value (assuming asymptotic chi-square) is 2.1%, i.e. this is not an acceptable goodness-of-fit and the model may be rejected. This implies that there are other sources of variation in survival.

Component	*N*	*GLM Estimate*	*s.e.*	*t*	*Prob.*	*Age-specific Survival*
Age class 01	9	0.103	0.203	0.51	30.6%	52.57%
Age class 02	9	1.682	0.385	4.37	**0.1%**	84.32%
Age class 03	8	1.269	0.377	3.36	**0.1%**	78.06%
Age class 04	7	1.050	0.439	2.39	**1.1%**	74.08%
Age class 05	5	1.299	0.651	1.99	**2.7%**	78.57%
Age class 06	5	0.182	0.606	0.30	38.3%	54.54%
Age class 07	2	0.69	1.22	0.57	28.7%	66.60%
Age class 08	1	6.2	13.7	0.46	32.4%	99.80%
Age class 09	1	-7.6	26.7	-0.28	61.0%	.05%

(Statistically significant coefficients shown in bold)

There is one point with high leverage (i.e. No. 28 - see Table 5.11). There are only two observations to estimate survival for age class 7 and this is one of them, thus it probably carries a high weight. There are three points with high residuals (i.e. Nos. 21, 34 and 39 - see Table 5.11). The first of these has a lower than expected survival and the other two are higher than expected. The survival estimate for the first age-class (i.e. fledgling to end first year) is equal to 52.6% and is statistically no different from a survival rate of 50%. The fitted GLM has the following form.

$\text{Logit}(S) = a_1\{\text{Age class 1}\} + a_2\{\text{Age class 2}\} + \ldots$

The inverse transform is:

$S = \exp[a_1\{\text{Age class 1}\} \ldots]/(1 + \exp[a_1\{\text{Age class 1}\} \ldots])$

Where the term {Age class i} takes on the value unity if age=i and zero otherwise. If the coefficient for a given age class is statistically equal to zero then the inverse reduces to:

$S = \exp[0]/(1 + \exp[0]) = 1/(1+1) = \tfrac{1}{2}$

The GLM estimates for the second to fifth age classes are significantly different from 0, i.e. the survival rates are different from 50%. This is not so for the subsequent (adult) age classes. This may be real, or it may be an artifact of a small sample size.

The upper age-classes are to be combined to see if this will yield estimates of survival which are statistically significant. The eighth and ninth age classes were combined. They were still not significant and so the seventh, eighth and ninth age classes were combined, these were also not statistically significant. This procedure was repeated until the fourth and subsequent age classes were grouped together to form a single '4+' age class. The results of fitting the GLM follow.

Component	*N*	*GLM Estimate*	*s.e.*	*t*	*Prob.*	*Age-specific Survival*
Age class 01	9	0.103	0.203	0.51	30.6%	52.57%
Age class 02	9	1.682	0.383	4.39	**0.1%**	84.32%
Age class 03	8	1.269	0.377	3.37	**0.1%**	78.06%
'4+' age class	21	0.856	0.289	2.96	**1.2%**	70.18%

(Statistically significant coefficients shown in bold)

The deviance of the residuals is 62.76 with 43 degrees of freedom (mean deviance = 1.460) and the associated probability value (assuming asymptotic chi-square) is 2.6%, i.e. this also is not an acceptable goodness-of-fit. There is one point with high leverage (i.e. No. 40 - see Table 5.11). This is an age class 2 observation with seven out of ten surviving which is low. There are two points with high residuals (i.e. Nos. 21 and 39 - see Table 5.11). The first has a low survival of 0/3 for age class 6 and the second has a high survival of 10/12 for age class 1. This gives a less variable estimate for the '4+' age class, but the goodness-of-fit it still is not adequate. A further possibility is to combine all age classes from the second year upwards, because they seem to be similar in magnitude (Figure 5.7). The resultant GLM analysis yields the following results.

Component	*N*	*GLM Estimate*	*s.e.*	*t*	*Prob.*	*Age-specific Survival*
Age class 01	9	0.103	0.203	0.51	30.6%	52.57%
'2+' age class	38	1.219	0.195	6.25	**0.10%**	77.19%

(Statistically significant coefficient shown in bold)

The deviance of the residuals is 65.88 with 45 degrees of freedom (mean deviance = 1.464) and the associated probability value (assuming asymptotic chi-square) is 2.29%, i.e. this also is not an acceptable goodness-of-fit. There are five points with high leverage (i.e. Nos. 16, 22, 35, 39 and 43 - see Table 5.11). All five are from age class 1 and suggest that it is not homogeneous. There are two points with high residuals (i.e. Nos. 21 and 39 - see Table 5.11). For the first the survival is too low, 0/3 for age class 6 while for the second it is too high, 10/12 for age class 1. This model gives a less variable estimate for the '2+' age class, but the goodness-of-fit is still not adequate.

An alternative approach is to assume that the age-specific survival estimates for each age class are not independent, but rather that they are some continuous function of age.

Age-specific survival utilizing a death function

In the preceding section survival was treated as a discrete function and estimated for each separate age-class. It is also possible to treat survival as a continuous function of age. To illustrate this, assume that survival is a function of age only and let the probability of death be described by a simple probability density function, to be called a death function. A death function, f(t) gives the probability that an individual will die in the interval $t \rightarrow t+dt$ as f(t)dt. Consider as the death function $f(t) = a \bullet \exp(-a \bullet t)$, i.e. an exponential decay. This function is chosen because it is both simple and realistic. This is a valid probability density function because it is everywhere non-negative and its integral over its domain (i.e. from 0 to ∞) is unity:

$$\int_{0}^{\infty} a\cdot e^{-a\cdot t}\,dt = a\cdot(e^{-a\cdot t}/-a)\Big|_{0}^{\infty} = 0-(-1) = 1$$

The probability that an individual will die in the age interval (i-1) to i is:

$$\int_{i-1}^{i} a\cdot e^{-a\cdot t}\,dt = a\cdot(e^{-a\cdot t}/-a)\Big|_{i-1}^{i} = -e^{-a\cdot i} -(-e^{-a\cdot(i-1)})$$

$$= +e^{-a\bullet(i-1)} - e^{-a\bullet i} = e^{-a\bullet i}(e^{a}-1) = A\bullet e^{-a\bullet i} \text{ where } A = (e^{-a}-1)$$

Hence the probability of survival over the same period is:

$$S_i = 1 - A\bullet e^{-a\bullet i}$$

To estimate the model parameter using GLM note that the Logit transform is:

$$\begin{aligned}
\mathrm{Logit}(S_i) &= \mathrm{Ln}(S_i/\{1-S_i\}) & &= \mathrm{Ln}[(1 - A\bullet e^{-a\bullet i})/\{1 - (1 - A\bullet e^{-a\bullet i})\}] \\
&= \mathrm{Ln}[(1 - A\bullet e^{-a\bullet i})/A\bullet e^{-a\bullet i})] & & \\
&= \mathrm{Ln}[(e^{a\bullet i} - A\bullet)/A] & &= \mathrm{Ln}[(e^{a\bullet i}/A) - 1]
\end{aligned}$$

This is a non-linear function and so difficult to fit using GLM. To simplify, expand as a power series:

$$\mathrm{Logit}(S_i) = \alpha_0 + \alpha_1\bullet i + \alpha_2\bullet i^2 + \alpha_3\bullet i^3 + \alpha_4\bullet i^4 + \ldots$$

The exact form of the coefficients, α_j (not shown here) is a complex set of logarithmic and exponential functions, all in terms of the parameter, a only. By reducing this function to a power series the exact form of the death function is lost and so this particular death function serves only to motivate the use of a power series. In fact, many different death functions can give rise to similar power series. The logit is fitted, via GLM, to the power series with as many coefficients as are statistically significant. A cubic fits the data with all the coefficients statistically significant:

Component	*N*	*GLM Estimate*	*s.e.*	*t*	*Prob.*
α_1	47	0.4652	0.0828	5.62	**0.1%**
α_3	47	-0.00875	0.00278	-3.15	**0.1%**

(Statistically significant coefficients shown in bold)

The deviance of the residuals is 70.54 with 45 degrees of freedom (mean deviance = 1.567) and the associated probability value (assuming asymptotic chi-square) is 1.3%, i.e. this model can be rejected - it does not provide a good fit to the data, even though each of the terms in the model is significant. This model cannot be used. There are three points with high leverage (i.e. Nos. 14, 15 and 28 - see Table 5.11) and these are all high-age categories with only one or two observations per age class. Thus are likely to contribute heavily. There are two points with high residuals (i.e. Nos. 1 and 21 - see Table 5.11) both of which have low numbers surviving - 2/9 and 0/3. These are much lower than expected. A number of other power-series were fitted, but are not shown. One of them, incorporating the α_0, α_1 and α_2 terms will be used below because it provides a better overall fit when temporal data are included.

Year-specific survival: Independent estimates

In the above analyses it was assumed that survival was a function of age alone. An alternative approach is to consider that survival is a function of time, i.e. calendar year, rather than age. This approach is valid in northern temperate climes in which most losses occur either during winter, or as a result of hunting pressure. These two factors can show considerable year-to-year variations which can be greater than age-specific variations (see brief review in Seber 1982: 525-527). The starting point in modelling temporal variations is to assume that survival is a function of year only and that the survival rate for any specific calendar year is independent of the survival in all other years. In a manner similar to that described above for estimating age-specific survival it is possible to estimate year-specific survival using a binomial model (Table 5.14). The year-specific survival rate increases strongly for the first four or five years (Figure 5.8) and this is caused by the 'ageing' of the population under study - until its age-distribution stabilizes (Figure 5.9).

Table 5.14

Year-specific survival estimates from observations of colour-ringed Cape Vultures in the South-western Cape. (Approximate 95% confidence limits estimated from Diem & Lentner 1970: 85 ff.)

Year	Number at Start	End	Survival rate	95% Confidence limits Lower	Upper
1979	9	2	22.2%	2.8%	60.0%
1980	8	4	50.0%	15.7%	84.3%
1981	17	9	52.9%	27.8%	77.0%
1982	24	16	66.7%	44.7%	84.4%
1983	25	21	84.0%	63.9%	95.5%
1984	31	23	74.2%	55.4%	88.1%
1985	35	30	85.7%	69.7%	95.2%
1986	44	26	59.1%	43.2%	73.7%
1987	35	21	60.0%	42.1%	76.1%
1988	18	14	77.8%	52.4%	93.6%

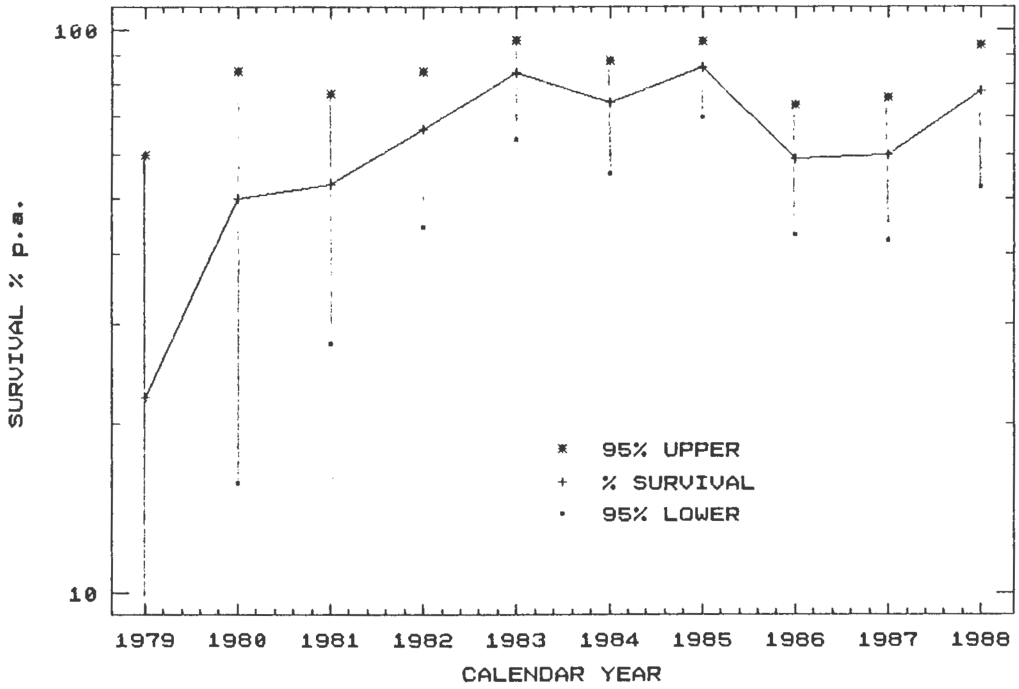

Figure 5.8 Estimates of survival as a function of calendar year for colour-ringed birds in the southwestern Cape.

It is possible to estimate the year-specific survival rates by fitting a GLM and this gives the results shown below.

Component	*N*	*GLM Estimate*	*s.e.*	*t*	*Prob.*	*Year-specific Survival*
Year: 1979	1	-1.253	0.802	-1.56	6.4%	22.22%
Year: 1980	2	0.000	0.707	0.00	50.0%	50.00%
Year: 1981	3	0.118	0.486	0.24	40.6%	52.95%
Year: 1982	4	0.693	0.433	1.60	5.9%	66.66%
Year: 1983	5	1.658	0.543	3.05	**0.2%**	84.00%
Year: 1984	6	1.056	0.410	2.57	**0.7%**	74.19%
Year: 1985	6	1.792	0.481	3.72	**0.1%**	85.72%
Year: 1986	7	0.368	0.307	1.20	11.9%	59.10%
Year: 1987	7	0.405	0.345	1.18	12.3%	59.99%
Year: 1988	6	1.253	0.566	2.21	**1.7%**	77.78%

(Statistically significant coefficients shown in bold)

The deviance of the residuals is 58.11 with 37 degrees of freedom (mean deviance = 1.571) and the associated probability value (assuming asymptotic chi-square) is 1.5%, i.e. this is not an adequate model and may be rejected. There are four points with high leverage (i.e. Nos. 1, 7, 16 and 22 - see Table 5.11) and these come from the first four years 1979, 1980, 1981 and 1982 when there are the fewest number of observations. There are four points with high residuals (i.e. Nos. 17, 21, 22 and 24 - see Table 5.11) where the survival rates are higher than expected.

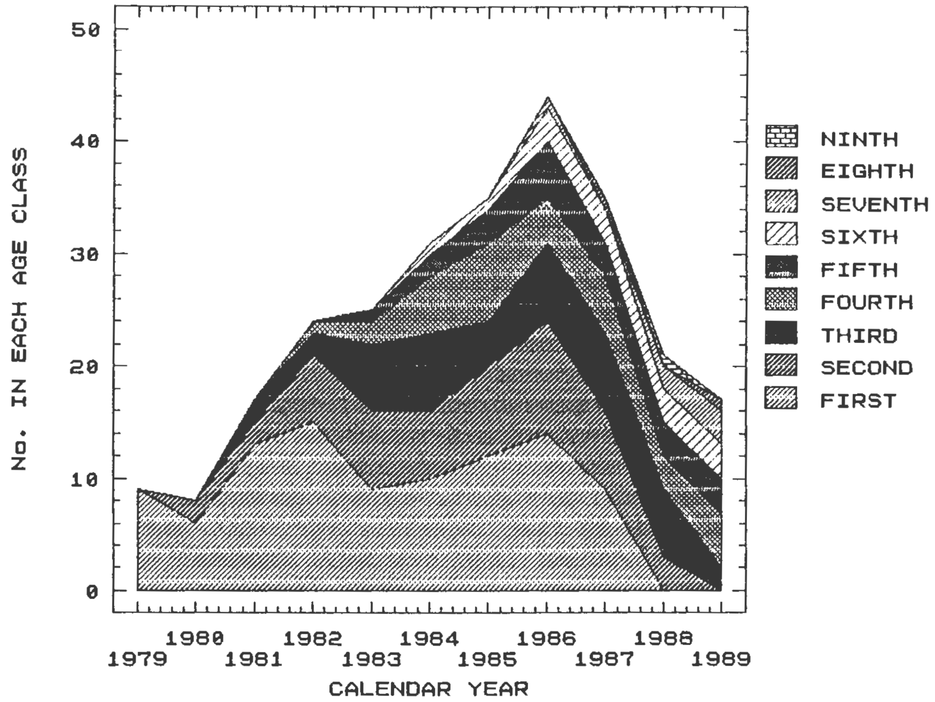

Figure 5.9 Age-composition of the population of colour-ringed Cape Vultures in the south-western Cape.

Thus it is seen that neither age-specific nor year-specific models on their own provide an adequate description of survival. This then suggests that survival may vary both as a function of age and time. This hypothesis is now tested.

Age- and Year-specific estimates: Independent estimates

The simplest joint model is one in which age-specific and year-specific survival rates are independent. This may be formulated as a GLM in the following manner.

$$\mathrm{Logit}(S_{ij}) = \mathrm{Ln}(S_{ij}/\{1-S_{ij}\}) = \alpha_0 + F_i + G_j$$

where F_i is age-specific factor for i^{th} age class
and G_j is year-specific factor for j^{th} year class

The reverse transformation is:

$$S_{ij} = \exp(\alpha_0 + F_i + G_j)/\{1 + \exp(\alpha_0 + F_i + G_j)\}$$

Fitting this model leads to results (not shown) which are patently ridiculous! This has happened because the age-specific and year-specific survival rates are not independent in a saturated model. Consider the link function used, with an arbitrary constant, τ added to each of the age-specific survival terms, but subtracted from each of the year-specific survival terms.

$$\mathrm{Logit}(S_{ij}) = \mathrm{Ln}(S_{ij}/\{1-S_{ij}\}) = \alpha_0 + (F_i + \tau) + (G_j - \tau)$$

This does not change the model but it greatly changes the estimates. A method for correcting this will be now be developed. A possible solution is to reduce the number of parameters, this will be attempted below.

It is obvious from the earlier analyses in this section that the survival rate of Cape Vultures in their second year, i.e. 84.3% (95% confidence limits: 71.4% to 93.0%) is significantly higher than that of first-year birds, 52.6% (95% confidence limits: 42.2% to 62.8%, Table 5.13). Thus a starting point for a model incorporating age and year effects could begin with the age-specific effects. Consider then an age-specific model with two, or more age classes. It is known for GLM that the change in deviance when adding a single additional term is exactly the chi-squared distribution with one degree of freedom. The following procedure is suggested (this is analogous to forward selection in multiple regression models): construct a GLM based on age-specific factors only. Then add the year-specific factors one at a time and for each one test to see which yields the largest decrease in deviance. Select the one year-specific factor which yields the largest decrease provided the decrease is statistically significant. From the results presented above (page 245), the simplest age-specific model is:

Component	*N*	*GLM Estimate*	*s.e.*	*t*	*Prob.*	*Age-specific Survival*
Age class 01	9	0.103	0.203	0.51	30.6%	52.57%
'2+' age class	38	1.219	0.195	6.25	**0.10%**	77.19%

(Statistically significant coefficient shown in bold)

For this model the deviance is 65.88 with 45 degrees of freedom and the mean deviance is 1.464. The year-effects are fitted one at a time. From the listing below it can be seen that only one year (i.e. 1985) contributes to a statistically significant decrease in the deviance.

Year	New deviance	Deviance change	Chi-squared (1 df)	Mean dev.
1979	62.05	3.83	n.s.	1.410
1980	65.60	0.28	n.s.	1.491
1981	65.63	0.25	n.s.	1.492
1982	65.58	0.30	n.s.	1.490
1983	62.13	3.75	n.s.	1.412
1984	65.43	0.45	n.s.	1.487
1985	**59.34**	**6.54**	**<0.05**	**1.349**
1986	63.14	2.74	n.s.	1.435
1987	63.50	2.38	n.s.	1.443
1988	65.87	0.01	n.s.	1.497

(Statistically significant coefficient shown in bold)

The year-specific effect for 1985 is included in the model and the procedure is repeated: all other year-effects are tested.

Year	New deviance	Deviance change	Chi-squared (1 df)	Mean dev.
1979	56.25	3.09	n.s.	1.308
1980	59.23	0.11	n.s.	1.377
1981	59.30	0.04	n.s.	1.379
1982	58.56	0.78	n.s.	1.362
1983	**54.26**	**5.08**	**<0.05**	**1.262**
1984	58.27	1.07	n.s.	1.355
1986	57.86	1.48	n.s.	1.346
1987	58.00	1.34	n.s.	1.349
1988	59.24	0.10	n.s.	1.378

(Statistically significant coefficient shown in bold)

It can now be seen that 1983 makes a significant decrease in the deviance and so it is also included in the model. The procedure was repeated yet again but no further year-effects were discovered. Thus the final model has two age-specific factors and two year-specific factors (Figure 5.10). The resultant combined model is:

Component	*N*	*GLM Estimate*	*s.e.*	*t*	*Prob.*	*Age-specific Survival*	*95% limits*
First years	9	-0.147	0.220	-0.67	25.3%	46.3%	(36% - 57%)
Age class 2+	38	1.118	0.289	3.88	**0.1%**	75.4%	(63% - 84%)
						Year-specific Survival	*95% limits*
Year: 1983	5	1.189	0.576	2.07	**2.2%**	76.7%	(52% - 91%)
Year: 1985	6	1.307	0.514	2.54	**0.7%**	78.7%	(57% - 91%)

(Statistically significant coefficients shown in bold)

The deviance of the residuals is 54.26 with 43 degrees of freedom (mean deviance = 1.262) and the associated probability value (assuming asymptotic chi-square) is 11.7%, i.e. this model has an acceptable goodness-of-fit. There are three points with high leverage (i.e. Nos. 23, 29 and 39 - see Table 5.11), all three having high survival values 7/7, 6/9 and 10/12 for age class 2 in 1983, 1 in 1983 and 1 in 1985 respectively. There two points with high residuals (i.e. Nos. 21 and 35 - see Table 5.11). The first has a low survival of 0/3 for age class 6 and the latter a high survival of 8/10 for age class 1.

Age-specific survival utilizing a death function; Adding year-specific variations

One way of tackling the indeterminacy resulting from a saturated model is to use a death function and to incorporate the temporal effects as in the following formulation.

$$\mathrm{Logit}(S_{ij}) = \alpha_0 + \alpha_1 \bullet i + \alpha_2 \bullet i^2 + \alpha_3 \bullet i^3 + \alpha_4 \bullet i^4 + \ldots$$

$$+ G_j$$

Where G_j is year-specific factor for j^{th} year class

Fitting a GLM to a second-order polynomial for the age-effects and including the year-effects as a factors produces the estimates shown on the next page.

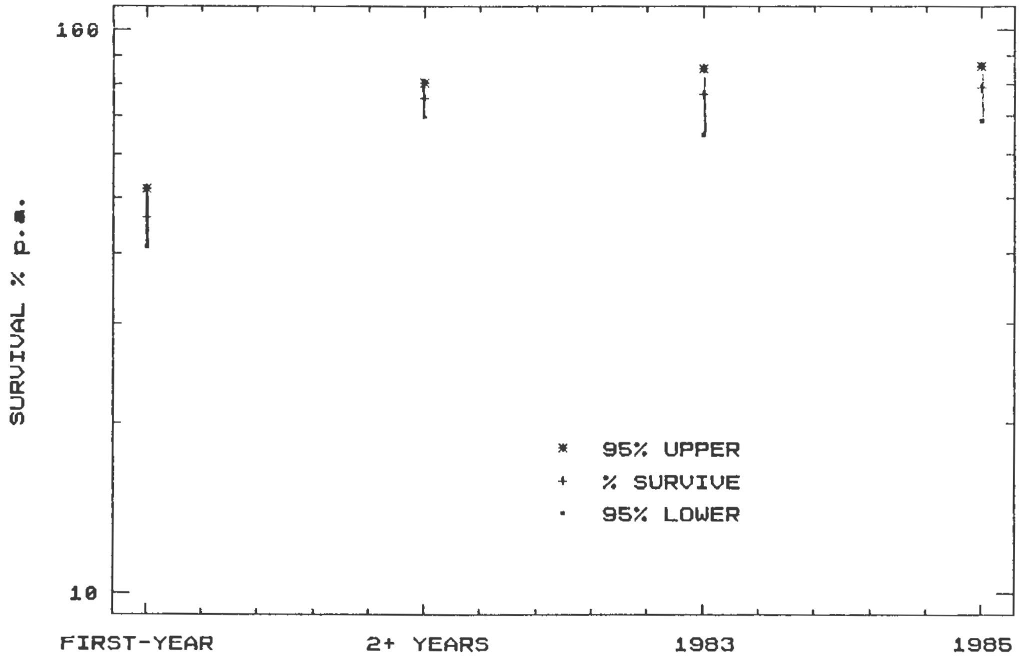

Figure 5.10 Estimates of survival as a function of age and calendar year for colour-ringed birds in the southwestern Cape.

Component	*N*	*GLM Estimate*	*s.e.*	*t*	*Prob.*	*Year-specific Survival*
α_0	47	-2.081	0.853	-2.44	**0.9%**	
α_1	47	0.955	0.335	2.85	**0.4%**	
α_2	47	-0.1264	0.0466	-2.71	**0.01%**	
Year: 1980	2	1.11	1.07	1.03	10.6%	75.21%
Year: 1981	3	1.204	0.942	1.28	10.4%	76.92%
Year: 1982	4	1.709	0.917	1.86	3.6%	84.67%
Year: 1983	5	2.476	0.982	2.52	**0.8%**	92.24%
Year: 1984	6	1.813	0.922	1.97	2.8%	85.97%
Year: 1985	6	2.595	0.951	2.73	**0.5%**	93.05%
Year: 1986	7	1.165	0.884	1.32	9.8%	76.22%
Year: 1987	7	1.174	0.905	1.30	10.1%	76.39%
Year: 1988	6	2.16	1.07	2.02	2.6%	89.66%

(Statistically significant coefficients shown in bold)

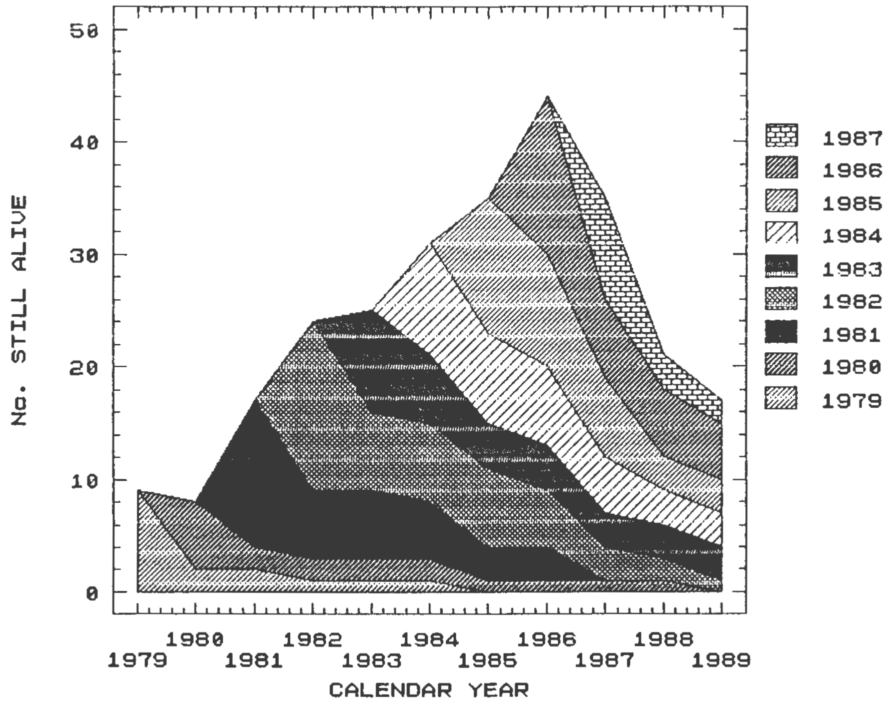

Figure 5.11 Survival of each cohort of colour-ringed birds in the southwestern Cape. Note that no birds from the 1979 and 1981 cohorts survived until the end of the study period.

The deviance of the residuals is 49.18 with 35 degrees of freedom (mean deviance = 1.405) and the associated probability value (assuming asymptotic chi-square) is 5.6%, i.e. this model (only just) has an acceptable goodness-of-fit, but its year-specific parameters are not all statistically significant. There are four points with high leverage (i.e. Nos. 1, 7, 16 and 22 - see Table 5.11), all these are low survival years for age class 1 indicating that this class is not homogeneous. There are two points with high residuals (i.e. Nos. 17 and 21 - see Table 5.11); the former is a high survival, 6/6 for age class 2 and the the other is a low survival for age class 6.

Starting with the age-specific model and adding the year-specific terms one at a time yields the following model.

Component	*N*	*GLM Estimate*	*s.e.*	*t*	*Prob.*	*Year-specific Survival*
α_0	47	-0.904	0.430	-2.10	**2.1%**	
α_1	47	1.060	0.323	3.28	**0.1%**	
α_2	47	-0.1339	0.0461	-2.91	**0.02%**	
Year: 1983	5	1.137	0.573	1.98	**2.7%**	75.7%
Year: 1985	6	1.241	0.512	2.43	**1.0%**	77.6%

(Statistically significant coefficients shown in bold)

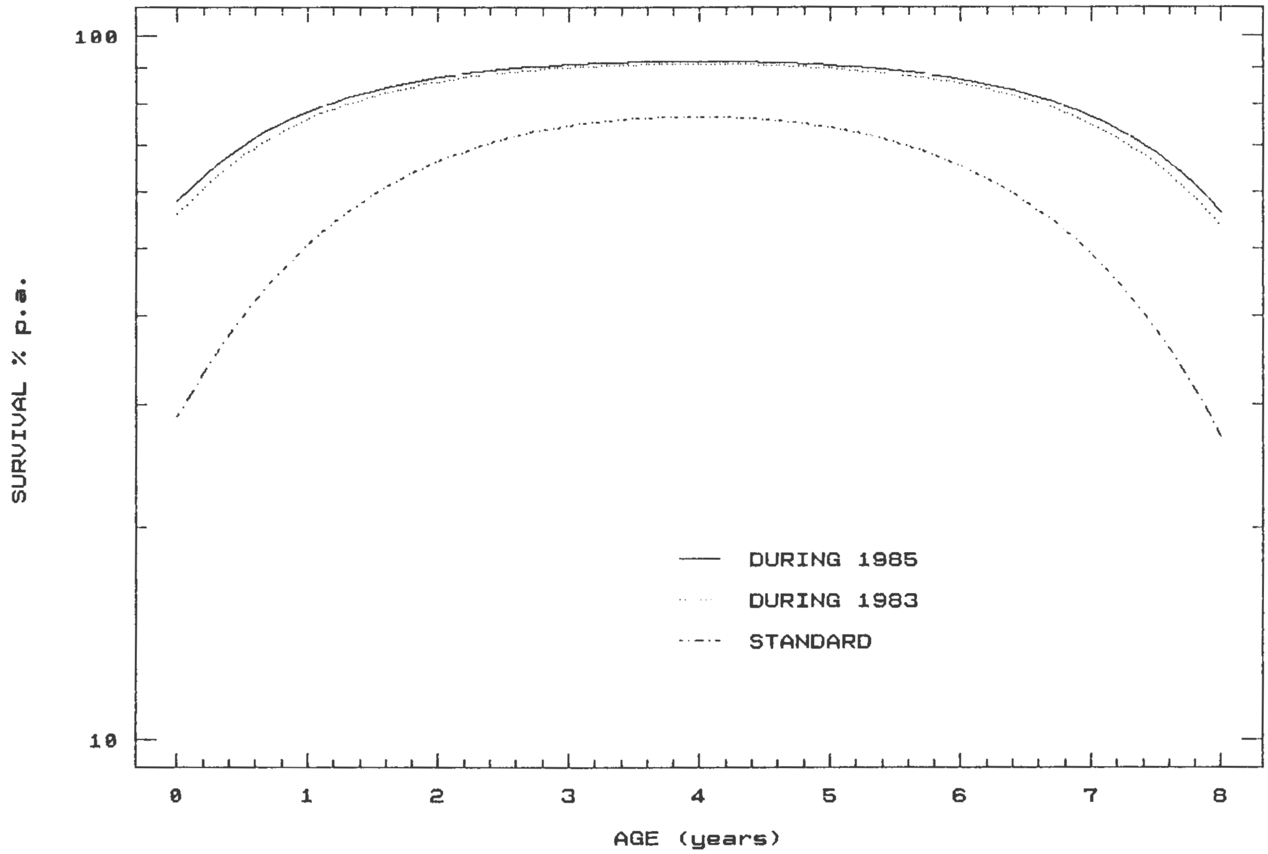

Figure 5.12 Estimates of survival as a function of age and calendar year for colour-ringed birds in the southwestern Cape.

The deviance of the residuals is 57.02 with 42 degrees of freedom (mean deviance = 1.358) and the associated probability value (assuming asymptotic chi-square) is 6.1%, i.e. this model (only just) has an acceptable goodness-of-fit. There are three points with high leverage (i.e. Nos. 23, 29 and 39 - see Table 5.11), all being high survivals, 7/7, 6/9 and 10/12 for age class 2 in 1983 and age class 1 in 1983 and 1985 respectively. There are two points with high residuals (i.e. Nos. 17 and 21 - see Table 5.11), the first is a high survival for age class 2 and the second is a low survival for age class 6.

Summary

Separate models based on age-specific survival rates and on year-specific survival rates were fitted to the data arising out of the resighting of colour-ringed Cape Vultures in the southwestern Cape. It was found that neither yielded models which adequately described the observations. This suggested that survival was possibly a function of both age and year. A number of models incorporating age- and year-specific survival rates were constructed and two of these were found to fit the observations in a manner which was adequate statistically. From these models it may be concluded that first-year survival is about 45-50% p.a. and that survival rises with age, but may fall for older birds. The calendar years 1983 and 1985 were good years for Cape Vultures in that they experienced higher survival.

5.3 The causes of mortality

"Much less is known about the mortality of raptors than about other aspects of their ecology". Newton (1979: 202-203). There are four reasons for this.

1) Mortality, unlike breeding, is difficult to observe because it occurs sparsely and unpredictably, both in space and time.
2) Mortality is difficult to attribute to its true causes. Assessing the cause of death is not easy when undertaken in field conditions, often by members of the public with little or no expertise.
3) The separation of proximate and ultimate causes of mortality is complex, even when undertaken by competent observers. A Cape Vulture, bearing the ring 508-00710, was reported as having been 'killed by dogs - could not fly' (SAFRING, *in litt.*). The proximate cause was an attack by domestic dogs, the ultimate cause may have been starvation or poisoning which prevented it from flying. It is even possible that the vulture had gorged itself at a carcass and could not get airborne due to windless conditions!
4) Quantifying the magnitude of different mortality factors is complicated by the fact that some dead birds are more readily reported (e.g. from electrocution) than others (e.g. shooting).

The causes of raptor mortality may be divided into 'natural' and 'unnatural' (Newton 1979: 207-208). This distinction is useful when investigating ways of halting population decline: natural causes of mortality are likely to continue, so conservation action must be directed at those causes thought to be unnatural. Natural mortality includes starvation, disease, predation, weather-related effects and natural accidents. Unnatural mortality includes electrocution, shooting, trapping, poisoning, collision with man-made objects, drownings, predation by domestic dogs, fire and mine-fields.

The causes of mortality to be described here apply only to birds which have fledged and older free-flying individuals, but not to younger individuals (i.e. eggs and nestlings) whose losses are described in the previous chapter.

Information on mortality and its causes in the Cape Vulture comes principally from the recovery of dead birds and anecdotal reports in the literature. When a ringed Cape Vulture is found in the field, its death may be reported to SAFRING, often via the Pretoria Zoo which is the ring return address. Sometimes the person reporting the recovery offers an explanation as to the cause of death, sometimes the Zoo or SAFRING requests an explanation and sometimes the Vulture Study Group posts a questionnaire. These requests often elicit further data.

Table 5.15

Numbers of ringed Cape Vultures recovered and classified by putative cause of death. (Only 'useful' recoveries are used - found > 10 km from colony)

Death code	Description	Number Killed	Relative frequency
005	Ring No. only	9	4.79%
009	Caught and killed	3	1.56%
010	Shot	12	6.38%
013	Shot:protect stock	3	1.60%
020	Poisoned	6	3.19%
021	Unintentional poison	3	1.60%
040	Illness	1	0.53%
043	Killed: ill	1	0.53%
046	Electrocuted	36	19.15%
050	Killed: animal?	1	0.53%
052	Killed by dog	1	0.53%
061	Collided: vehicle	1	0.53%
067	Collided: Mast	1	0.53%
068	Collided: building	1	0.53%
069	Flew into fence	9	4.79%
092	Drowned	22	11.70%
099	Cause unknown	72	38.30%
753	Ring removed	1	0.53%
?09	? Caught & Killed	1	0.53%
?10	? Shot	1	0.53%
?20	? Poisoned	3	1.56%
		Total 188	

The reported 'cause of death' is placed in one of 18 categories (Table 5.15) as per a schedule devised by SAFRING (T.B. Oatley pers. comm.). Where there is no direct evidence, but circumstances strongly suggest a possible cause of death then this is preceded by a question mark (3 categories).

Unfortunately, 38% of Cape Vulture recoveries have no reported cause of death while 5% had the ring number only reported (Table 5.15). Eliminating those ring recoveries with no meaningful 'cause of death' leaves 107 birds with a well-defined 'cause of death' and 5 with a 'strongly suspected cause of death'.

Natural causes of mortality.

Consideration is given first to those factors which can reasonably be called 'natural' in that they have operated since time immemorial and are independent of the 'hand of man'.

Food availability and Starvation

Ultimately, food is always a limiting factor because it sets an upper limit to the maximum potential population size (Newton 1991: 7). Because the availability of food varies both in space and time and because non-breeding birds are not tied to any particular colony, and hence to no particular region, the limitations of food will act in quite different ways on different segments of the population. As an example, inexperienced young birds arriving at a carcass will generally be out-competed by older, more experienced birds (McGahan 1972; Mundy 1982: 247-248). Even when there is a whole carcase, many birds may still not be adequately fed (Mundy 1984: 110); it is to be expected that when birds are short of food they will die of starvation. It is now known that starving birds are also susceptible to a variety of other proximate causes of death, including disease (Mundy 1984: 110). None of the 'useful' recoveries was reported as having died of starvation.

Disease and parasites

Adult vultures, in particular, are known to be resistant to a range of mammalian diseases (Mundy 1984: 110) including botulism (Cohen 1970), anthrax (Houston & Cooper 1975) and other bacteria (Schlatter *et al.* 1978). The Cape Vulture is the host of a species-specific tick *Argas zumpti* (Hoogstraal, Kaiser & Kohls 1968) and other ecto- and endoparasites. In the south western Cape, black flies (*Prosimuliium* sp.) are known to feed on nestlings (Robertson 1986 and references therein), but it is not known if they also infest adults. Cape Vultures are known to be infected by avian haematozoa (Boshoff & Currie 1981); blood smears have revealed the presence of one or more species of *Leucocytozoon* (Boshoff & Currie 1981, Robertson 1986). In an experimental situation it was possible to transmit *Sarcocystis* sp. from an impala to a Cape Vulture (Markus, Daly & Mundy 1984; Markus, Mundy & Daly 1985) and Cape Vultures are now thought to be one of the final hosts for two *Sarcocystis* spp. in the wild. Thus, while it is known that Cape Vultures carry many endo- and ectoparasites, it is not known if they contribute to mortality.

Predation and Cannibalism

Most proven instances of predation are on eggs and small nestlings (e.g. Black Eagles *Aquila verreauxii* taking eggs and nestlings, Bowen 1970; Mundy, Robertson, Komen & O'Connor 1986). There are some observations of the occasional 'predation' attempt on free-flying Cape Vultures (R. Neilson in Anon. 1959; Pitman 1960; Mundy, Robertson, Komen & O'Connor 1986). It is, however, most unlikely that predation will be a numerically substantial cause of mortality for adult Cape Vultures.

Vultures are rarely cannibalistic and only one case has been documented (Mundy, Butchart, Ledger & Piper 1992: 276). At Mtzikaba, in the Transkei, a large nestling was observed to feed on a dead adult near its nest (pers. obs.). In addition there are two other records of vultures eating other vultures - in one case the dead vulture was a road casualty but in the other the cause of death was not noted (Mundy, Butchart, Ledger & Piper 1992: 276). Unless the vulture was killed by other vultures it is not cannibalism, strictly speaking.

Weather

Rain influences vultures in a number of ways. First, during periods of continuous rain vultures are unable to get out and forage and feed (Mundy 1984: 110). Secondly, heavy and persistent rain could possibly cause vultures' plumage to become wet and this in turn causes heat loss and increases energy use, though there is no documentary evidence for this in the Cape Vulture. Thirdly, rain when combined with sub-zero temperatures can cause vultures to ice-up (Karner 1981). It sometimes happens that on days when vultures sally out to forage, they get caught in thick mist on their return journey. They are still able to fly under these conditions, and do so by 'hugging' the upper contours of ridges and mountains (pers. obs.), but it is likely that they are vulnerable to collision under these circumstances. This hypothesis has been advanced as an explanation for collisions with towers, power lines and fences (see below) but it is also reasonable to assume that under these conditions natural accidents could occur. No numerical estimate can be made of the influence of weather effects on population dynamics, but it is suspected that it is small.

'Natural' Accidents

There are two situations in which vultures can come to blows. On the ground when feeding, loafing or bathing, and in the air when flying. When feeding at a carcass vultures, interact vigorously with each other and sometimes do each other an injury (Mundy 1984: 110). Cape Vultures are superb flyers in even the strongest gusting wind, but occasionally come to grief when trying to land in these conditions. During a fierce 'Berg wind at Colleywobbles two adults were blown off their nests; one managed to get control of itself and sailed away but the other was thrown down into the forest below whence it slowly extricated itself (pers. obs.). On many a hot afternoon, a group of birds at a colony will take to the air and sail around together in a circle, as if they were all in a circus. Sometimes not all the birds go in the same direction and collisions have been noted (pers. obs.). It is likely that both Lions and hyaenas kill the odd vulture (Baldwin 1985), and that this fact is under-reported by most bird-watchers even though it must have been seen many times by people watching mammalian predators and scavengers feeding at carcasses. No numerical estimate is possible for the impact of natural accidents on the population dynamics of the Cape Vulture, but it is likely to be small.

Senility or Senescence

There is now considerable evidence to show that as birds get older they become weaker, and so are more vulnerable to various forms of mortality (Mundy 1984: 111; Newton 1989: 458-462; Partridge 1989: 433-434; Wooller, Bradley, Skira & Serventy 1989: 416). In theory, at least, it should be possible to estimate this effect by monitoring a sufficiently large number of known-age, colour-ringed birds. This is not yet possible because too few nestlings have been ringed with long-lasting colour rings (see sections 5.2.1 and .2 above).

Non-imprinting on nest site

Once a fledgling leaves the nest, it still needs to get back to its natal ledge to be fed by its parents for it is dependent upon them for some time (Robertson 1985) - called the post-fledging dependence period (PFDP). During the PFDP, parents will only feed their own nestling at their nest site, nowhere else (Boshoff & Robertson 1985). Fledglings which try to land at other nest sites are repulsed (pers. obs.) and fledglings which beg from their own parents at places other than the natal nest-site are not fed (Boshoff & Robertson 1985). Thus fledglings which do not imprint on their nest sites may well die (loc. cit.).

Unnatural causes of mortality

The range of mortality factors acting on raptors in general (Newton 1979: 207-208), and vultures in particular (Houston 1987; Mundy 1982: 272, 1984: 111), includes diminished food supply, electrocution, poisoning, drowning, disturbance, persecution, collision with vehicles, collision with man-made structures, domestic dogs, fire and mine-fields.

Reduction in the food supply

In those far-off days before commercial agriculture, Cape Vultures fed from the carcasses of many different species of antelope (Mundy 1984: 111) and it is possible that during the 2 000 years before the arrival of the settlers from Europe, the Cape Vulture also fed from the bodies of dead domestic sheep and cattle (Robertson & February 1986). Prior to the advent of commercial agriculture, the Cape Vulture was able to feed from a food source which was predictably, if not uniformly, distributed in space and time. Since most of southern Africa has been turned over to commercial agriculture, several important changes have occurred. The number of dead animals available to vultures has deceased as a result of improved animal husbandry (Boshoff & Vernon 1980, 1984; Brooke 1984). A decrease in the number of carcasses available to vultures has been implicated in the decline of vulture populations in southern Europe (Cheylan & Thibault 1981) and in Israel (Leshem 1985a). Another exacerbating factor has been the changing attitude to the disposal of the carcasses of domestic stock, with a trend to burying them (Brooke 1984).

Because of overgrazing there are places in southern Africa (e.g. Namibia) where the predominant vegetation has changed from an open tree-savanna to thick-bush. As a result it becomes difficult for griffons, with their large wing-span, to land and take off. Consequently, vultures cannot exploit a food source which should otherwise be freely available to them (Brown 1985a).

It is obvious that the range of prey species available to most Cape Vultures has been reduced from over ten wild natural herbivores to four or five domestic species. It is not clear if this represents a reduction in food quality. However, it is suspected that the quality of domestic stock available to scavenging birds has declined as a result of the growth hormones and antibiotics fed to them, and the various bacteriacal, insecticidal and acaricides placed on them (Mundy 1984: 111; see also the discussion below concerning poisons).

There is no direct evidence for a population decline as a result of diminishing food supply. However, it is possible to investigate those roosts and colonies at which there have been documented declines in population and ask the question 'What caused these declines?'. As a second line of evidence, consideration can be given to those regions which have seen a real contraction in the species' range.

Electrocution

Vultures, like many other large birds (e.g. Golden Eagle *Aquila chrysaetos* Benson 1981), are particularly vulnerable to electrocution because of their great size and predilection for perching on electricity power pylons. As a consequence of their tendency to roost gregariously the numbers of birds electrocuted in any one incident may be high because they are all electrocuted together even though only one bird may have been the source of the electrical short-circuit[1].

Electrocution of the Cape Vulture has been recorded on both 11 kV and 22 kV lines in the Cape (Boshoff & Vernon 1979), but all the lower voltage lines (i.e. 11 kV, 22 kV, 66 kV and 88 kV) are known to be dangerous to large raptors (Ledger 1978, 1988; Ledger & Annegarn 1981). One tower in particular, the 88 kV kite-frame[2], has been responsible for most of the Cape Vulture deaths, estimated at between 92% (Ledger 1984) and 96% (Ledger

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[1] P.J. Mundy (*in litt.*) comments that this is unlikely, in his opinion.

[2] Photographs of the various structures referred to here may be seen in Mundy, Butchart, Ledger & Piper 1992: 371-377.

& Annegarn 1981). The higher voltage lines (i.e. 132, 275 and 400 kV, which are mostly supported by lattice towers) are considered to be almost totally safe for vultures (Ledger 1978). Nevertheless at least one Cape Vulture has been electrocuted on a 132 kV line (Ledger 1980). There are extensive networks of the lower voltage lines across southern Africa. In the Cape Province there were about 9962 km and 5004 km of 11 kV and 22 kV lines, respectively, in 1978 (Boshoff & Vernon 1979).

In surveys of the use of electricity towers as roosts by the Cape Vulture it has been found that they tend to use only a few specific towers along a line, and that they tend to re-use those towers repeatedly over many years, ignoring all others in the vicinity (Ledger 1984). This has also been noted for the Eurasian Griffon *Gyps fulvus* in Israel (Leshem 1985a, b). Cape Vultures tend to frequent those lines in the western Transvaal that run though cattle and game ranching areas, while they avoid the lines through extensive crop-lands (Ledger 1978). Once it was recognised that electrocutions have tended to occur on specific lines and at specific towers, it was much easier to target corrective action (loc. cit.). The most direct action has been to add protection to the offending towers. A most effective solution has been to replace the line with a safer construction. This is not always possible, and sometimes a better line (in terms of being vulture-friendly) has been built parallel to the first. This is often successful, except when stock losses occur close to the old line and it is then used again as a perch prior to, or subsequent to feeding, at which point it becomes a danger to the birds (J.A. Ledger pers. comm.)

An approximate estimate has been provided for the total loss of Cape Vultures to electrocution - 500 birds dead in five years (Ledger 1980). It is likely that the early estimates of numbers killed along Eskom (Eskom is the electricity supply utility for South Africa) lines are grossly under-counted because the linesmen did not keep their logbooks (Ledger & Annegarn 1981). By way of comparison, in a two year period during the early 1980s, nearly a quarter of the Eurasian Griffon *Gyps fulvus* population of Israel was killed by accidental electrocution (Leshem 1985a). At about the same time, a large number of Egyptian Vultures *Neophron percnopterus* and some Lappetfaced Vultures *Torgos occipitalis* were electrocuted at Port Sudan (Nikolaus 1984).

Most of the electrocutions reported in the literature occurred in the Transvaal with a few in the Cape, and most were reported in the 1970s (Boshoff & Vernon 1979: 102-104; Jarvis 1974; Ledger & Annegarn 1979, 1981; Markus 1972). The heaviest concentration was in the western Transvaal (see Chapter Six below). Two aspects of this western Transvaal concentration are particularly interesting. First, most of the birds killed were first-years and secondly, they came from every corner of the species' range, except the south west Cape and Namibia (Ledger 1982, 1984).

The western Transvaal has acted as an electrocution-induced mortality 'sink' for much of the population of young Cape Vultures. Consequent on this is the notion that 'colony protection' is not enough to conserve this component of the population (Ledger 1982).

When birds are found below power-lines, it is generally assumed that they have been electrocuted or have collided with the line or tower, but it is also remotely possible that they could merely have gone to roost on the tower, died of another cause and dropped to the ground. In the opinion of Eskom officials, there are few collisions with lines because almost all the dead birds are found directly below towers (Ledger & Annegarn 1981). In the Orange Free State, a number of dead Cape Vultures found below power-lines, were shown upon chemical analysis, to have died of strychnine poisoning (Colahan 1989). Thus searching below power lines for birds which may have been electrocuted, or collided with the lines, could also yield evidence for birds which have died from other causes. It is likely that this could be a useful monitoring tool, and it would be highly desirable to make this part of the Eskom linesman's brief.

Much effort on the part of Eskom has been devoted to making their lines and support structures bird-friendly (Hobbs & Ledger 1986a, b, 1988). The most successful technique has been the total removal of the poorly designed structures, especially the 88 kV kite-frame and 88 kV H-frame towers (loc. cit.). An interim solution has been the modification of the offending towers by affixing a long wooden pole to the top of the kite-frame tower (Ledger 1984). While modifying a tower is an effective solution it is not a total solution because when the extended wooden perch is full, new arrivals will tend to sit inside the frame - hence becoming susceptible to electrocution. This, and various other modifications have been tried in other parts of the world and have worked for many large birds (Olendorf, Miller & Lehman 1981; Reinert 1984).

Another hypothesized danger to birds which roost or breed near power lines arises from the electromagnetic fields induced by ultrahigh voltage power-lines (Berliner 1982), though this has since been discounted as a serious concern (J.A. Ledger pers. comm.).

This chapter is focused on those factors which negatively impact on the Cape Vulture. However, it should also be noted that the extensive network of power lines, and their support structures, through those pastoral regions of southern Africa which are far from Cape Vulture cliff-based roosts and colonies has enabled this species to extend its range (Ledger 1978; also see Chapter Three above and Chapter Six below) and for the African Whitebacked Vulture *Gyps africanus* even to breed on the pylons (Ledger & Hobbs 1985).

Poisoning

Poison as a source of unnatural mortality in the Cape Vulture has been known to have killed many individuals over a much longer period of time, and over a greater part of the species' range, than electrocution. For more than two centuries, it has been a common practice in southern Africa to use a dead animal, laced with poison, as a bait for mammalian carnivores who are suspected of taking domestic stock. In many cases the target species, being a predator rather than a scavenger, is not harmed. However, vultures have been killed in this way by their hundreds and even thousands (Mundy 1984: 111).

In the Cape Colony, during the nineteenth century, poison was regularly used in farming operations (e.g. Brooke 1984; Bryden 1889; de Jager Jackson Ca. 1920; Leyland 1866; Martin 1890). This practice was carried forward into the first half of the twentieth century (e.g. Boshoff & Vernon 1979: 99; Daily Dispatch 1924; Godfrey 1934; Ledger 1977). There are few reports of the use of poison in the Cape Province during the period 1950-1969 (but see Boshoff & Vernon 1979: 99). During the decade 1970-1979 a number of incidents were noted (e.g. Baron 1981; Boshoff & Currie 1981). While it is not possible to provide a quantitative estimate of the number of Cape Vultures poisoned since 1980 in the Cape, it is possible to state that recent incidents of Cape Vultures dying from poison have been widely publicised and have received much attention in the news media (e.g. Agricultural News 1984). There still are a substantial number of vultures being poisoned in the Cape (e.g. Moorcroft 1984; Vernon 1984).

There do not appear to be records for Cape Vultures being poisoned in the Transvaal in the nineteenth century, but poisoning was noted in the first part of this century (Taylor & Bucknill 1907). From the 1970s, poisoning has become a serious source of unnatural mortality for those Cape Vultures inhabiting the Transvaal (e.g. Anon. 1980; Mundy & Ledger 1980, Benson & Dobbs 1984) and is still a major problem (e.g. Robertson & Butchart 1990).

It is only in recent times that Cape Vultures have been recorded as poisoned in Botswana (e.g. Borello 1985), but this could merely have gone undetected earlier. This situation is similar for Zimbabwe where most poisoned vultures have been of species other than the Cape Vulture (e.g. Morris & Mundy 1981).

In Namibia there has been a widespread use of poisons for carnivore control and Cape Vulture deaths have been noted throughout the third quarter of this century (C.J. Brown pers. comm.; Brown 1980, 1985b).

It is likely that deaths from poison have been under-reported for the Cape Vulture in Natal in view of the widespread use of poisons in the Province, especially among smallstock farmers (Brown & Piper 1988).

The use of poison in the Orange Free State is also widespread (C.J. Brown pers. comm.) and has led to many Cape Vultures having been poisoned this century (e.g. Colahan 1988; Roos & Roos 1988; van der Byl 1987; van Heerden 1980).

Thus it may be concluded that poisons have been used over most of southern Africa where the Cape Vulture occurs and for the best part of 150 years. It is difficult to imagine the carnage that this has caused.

The range of compounds used to poison vultures deliberately is large, as is the list of chemicals which are poisoning vultures in an incidental fashion. To date, 14 compounds can be listed, but there may be some overlap between formal chemical names, commercial formulations and common farming names. Each of the products which has been implicated in causing Cape Vulture mortality is briefly described below, together with whatever incidental information is available

Blue death is a mixture of carbaryl and gamma BHC, and has been implicated in the poisoning of vultures for sale to the traditional medicines trade (van Jaarsveld 1987).

Coopex is an organophosphate used to treat sheep which have infestations of blowfly maggots, but is sometimes fatal to Cape Vultures (Vernon 1987).

Curaterr is the carbamate insecticide *carbofuran* (Group I poison: Ledger 1985) which has been used to poison Lion, Warthog and vultures in eastern Caprivi (Anon. 1981). It is not known if it has impacted on the Cape Vulture.

Cyanide is a well-known poison which acts more strongly against vultures than carnivores (Wiemeyer, Hill, Carpenter & Krynitsky 1986). It has been used by poachers to kill vultures deliberately in the Kruger National Park (van Jaarsveld 1987).

Dazzel contains the organophosphate *diazinon* (Ledger 1985) and is used to poison grain put out as bait for cranes (Vernon 1987) - it is not known if it kills vultures which could prey on the dead cranes. It is also used to control maggots on sheep, and so causes vulture deaths when the dead sheep is eaten by vultures (Ledger 1985).

DDT and associated compounds (DDE, DDD=TDE, t-DDT, PCB, Aldrin and Dieldrin) are organo-chlorine compounds which have been shown to have deleterious effects on a wide range of raptors (Newton 1979). Some of these compounds have been found in Cape Vulture eggs collected in the south western Cape, Botswana and Transvaal (Boshoff & de Kock 1988; Mundy, Grant, Tannock & Wessels 1982; Robertson & Boshoff 1986). The eggs showed some shell thinning. It is likely that the adults themselves carried these contaminants, but it is not known what deleterious effects they could have on the survival of adult vultures.

Dips, acaricides and insecticides may cause accidental poisoning (Boshoff & Vernon 1979: 101 ff. but the specific compounds are not known).

Lu jet (also spelt Lu-jet) is sprayed on sheep to combat the 'brommer' plague (Boshoff & Vernon 1979: 101 - but the specific compounds are not known) and is injected into fowl eggs to kill ravens (Vernon 1987).

Lybacide (or Lebaycid) is injected into fowl eggs to kill ravens (Vernon 1987).

Pesticides - see DDT above.

Strychnine is an alkaloid (Brown 1985b) and has been the most lethal compound used for the last 150 years over much of southern Africa for 'so called' predator control. In a recent study of farmers of the Transvaal, it was found that ten of 21 farmers (i.e. 47%) still used strychnine, putting it in carcasses, pieces of meat or even in dead doves (Berliner 1984). In earlier times, many vultures were poisoned: 'there they lay, those dead vultures, in scores, in hundreds! in all stages of decay' (de Jager Jackson Ca. 1920: 281 referring to a Karoo colony in about 1870); 'The Ostrich-farmer should bear in mind that strychnine used *ad libitium* is one of his best friends' (Douglass 1881). At the turn of this century, a number of 'poison clubs' were formed with the deliberate aim of eradicating carnivores and scavengers (Finch-Davies 1920; Haagner & Ivy 1907). By 1860 it was acknowledged that strychnine was a cause of decline for some other vulture species (FRS 1860, quoting Sir Andrew Smith). Strychnine is still a serious problem (e.g. Dobbs & Benson 1985) and it can be obtained readily over much of southern Africa (Brown 1985a, b).

Temik was used to kill a Lion and vultures in Kruger National Park (van Jaarsveld 1987: 101 - but the specific compounds are not known).

Topclip is used to dose lambs for maggots and in one case killed '28 vultures, 16 crows and the lamb' (Boshoff & Vernon 1979: 101 - but the specific compounds are not known).

It is likely that at least 500 vultures of three or more species were poisoned in the period 1979 to 1984 (Ledger 1985). Assuming that this is a substantial under-count (loc. cit.), then as a rough estimate it is suggested that about 100 Cape Vultures were poisoned each year[3]. In assessing the impact of poisoning, it must be remembered that killing an adult during the breeding season is likely also to lead to the death of its progeny (van Jaarsveld 1987). In 1984, a campaign was initiated to monitor the Namibian Cape Vulture colony on the Karakuwisa cliffs of the Waterberg. Four pairs bred successfully, but one nestling died at about the time two adult Cape Vultures were found dead (possibly drowned) in the Eastern National Water Carrier - it is suspected that they were the parents (Brown 1985a) [4].

Cape Vultures die because some farmers deliberately put poison in the bodies of dead animals from which they are likely to scavenge. This need not be done by the majority of farmers for 'the actions of only a very few farmers can have disastrous consequences for the vultures' (Vernon 1987).

As the conservation ethic permeates the community of pastoral farmers, it is likely that there will be fewer incidents of direct poisoning. Unfortunately, at the same time, economic conditions are likely to become even more stringent and this will drive farmers, especially of small stock, to use even more medicines in their animal husbandry. Naturally, Cape Vultures

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[3] On the other hand Mundy, Butchart, Ledger and Piper 1992: 432, Table 45 estimate 127+ Cape Vultures killed during the period 1982-1992, i.e. just under 12 p.a.

[4] P.J. Mundy (*in litt.*) notes that during the early part of the nestling period at least one of the adults stays at the nest - thus it is unlikely that the two birds killed were from the same pair.

will ingest these when they eat from livestock carcasses. This has led Vernon (1987) to opine of poisoned vultures: 'The Cape Vultures ... were already so full of toxins that a little more tipped the balance.'

Drownings

Contrary to popular belief, vultures are fastidious creatures bathing often (Butchart 1988). Farmers' dams, water reservoirs, and stock watering troughs thus often attract vultures as well as many other bird species. The drowning of birds in these structures has been noted in North America (e.g. Craig & Powers 1976; Chilgren 1979) and Britain (Johnson 1991). In southern Africa, five major incidents of Cape Vultures drowning in farmer's dams and reservoirs have been reported in the literature (Table 5.16).

Why do vultures drown in reservoirs? A plausible reason has been advanced by Ledger (1979).

> A record from the Ventersdorp district of the Transvaal ... On 22 June 1978 a farmer found 36 Cape Vultures in a circular cement reservoir containing about 60 cm of water. Nineteen were alive and were extricated; after drying their feathers while perched on the surrounding anthills and rocks, they flew away. Of the 17 dead birds three had been ringed; one was 3 years old, the others 2 years and all came from the same breeding colony (Skeerpoort). The 2-year old birds had been reared in adjacent nests. It is now suggested that these mass drownings result from the very intimate lifestyle of Cape Vultures, which breed, roost, feed and travel cross-country in very close-knit groups. Like feeding activity, normally triggered by the actions of one individual that releases the feeding response in the group, it is suggested that bathing too is a group activity, triggered by the first individual to enter the water. If this water happens to be in a partly full reservoir with vertical sides, the birds cannot escape and drown.

In addition to wanting to bath and drink, vultures may enter the water to cool off (see Chenaux-Repond 1976 for raptors). This suggestion is plausible as it is thought that vultures are heavily insulated to withstand the extreme sub-zero temperatures which they experience when flying at great altitude (Houston 1986); this in turn implies that they will be less well adapted to withstand hot conditions, so that they will need to find behavioural strategies to cope with overheating.

How can drownings be prevented? For drinking troughs it is suggested that floating wooden, or hollow plastic grids be placed therein (Johnson 1991) and for reservoirs a floating walkway (or plank) should be attached to the wall (Butchart 1988).

Table 5.16

Recorded incidents of Cape Vultures drowning.

Place	Structure	Date	Killed	References
Queenstown	Reservoir	1963	13	Boshoff & Vernon (1979: 99, No. 3); Ledger (1979)
		1972	3	
		18-05-1975	34	
		26-05-1975	14	
Adelaide Waterfall Roost	Reservoir	1960s	12	Boshoff & Vernon (1979: 99, No. 7)
Sterkstroom	Unknown	05-1977	Some	Boshoff & Vernon (1979: 99, No. 9)
Ventersdorp	Reservoir	22-06-1978	17 Released 19	Ledger (1979)
Eastern National Water Carrier	Canal	11-1984	2	Brown (1985a)

Disturbance and Persecution

Vultures are often disturbed in their innocent endeavours at the nest, and while roosting, bathing loafing or feeding. This is often caused by urban tourists and such disturbance is likely to increase in the future (Mundy 1984: 112). Small boys rolling stones down onto breeding cliffs kill both nestlings and adults (pers. obs.; Verdoorn 1991). Vultures have been used for target practice (in one case to impress a girlfriend, A. Weichman pers. comm.) and have also been shot and killed for sale to the traditional medicine trade (Cunningham 1990).

Collision with vehicles

Vultures are attracted to roadsides where they feed on animals killed by road vehicles (pers. obs.). Sometimes the vultures themselves are killed by the passing traffic (Spiker 1936, Sprunt 1937). It is conjectured that this can happen in three ways: a vulture can fly into a vehicle when crossing a road (e.g. van Rhyn in Anon. 1967) or attempting to land; it can be knocked down when flying up in the face of the oncoming traffic; and it can be run over by a vehicle when foraging on a carcass, or loafing nearby.

Collision with man-made structures

For over one hundred years it has been known that tall towers, their wire stays and suspended cables are hazardous to birds, both local and migrating (e.g. Benson & Dobbs 1985; Larkin 1988; Norman 1982, 1987). It is also known that buildings atop mountains can be dangerous to birds (e.g. Buckelew, Hutton & Allen 1986). Electrical power lines and other 'aerial' cables can be a serious threat to birds (e.g. Miquet 1990), but this view is not held universally (Hobbs 1987).

It is known that specific communication towers and their stays have been greatly detrimental to Cape Vultures. A 230 m high tower erected by the South African Broadcasting Corporation (SABC) on the Kransberg, near Thabazimbi, killed 49 (Dobbs & Benson 1982, Benson & Dobbs 1985), or 55 (Benson & Dobbs 1984) Cape Vultures in December 1981, and 20 were killed in the period January to June 1984 (Correia 1984). In the Orange Free State, on 10 July, 1987, two Cape Vultures were found near a microwave tower, but it is not known whether they died from collision or poison (Roos & Roos 1988).

It is possible to reduce the number of birds killed at communications towers by placing bright orange balls on the supporting stays (e.g. Benson & Dobbs 1985; Celliers 1984 - at the Kransberg tower). These are also called 'Bird Flight Diverters', and have been recommended for use with electrical conductors (Ledger 1989). It was suggested above that the provision of (or removal of) power lines and other 'aerial' wires in vast treeless plains can markedly alter the distribution of a number of bird species. This has also been noted for North America (Muir 1983).

Weather: Dense mist or fog

Vultures can become airborne and fly even in dense fog, often by staying close to the ground and using slope draft to follow the contours around hillsides and mountains (pers. obs.). In poor-light situations, such as these, they are particularly susceptible to collision with telecommunication towers, their supporting wire guys, power lines and fences. But even in clear conditions, recently fledged Cape Vultures are susceptible to collisions with wires and fences (Benson & Dobbs 1984, 1985).

Killed by dogs

When feeding at a carcass, while waterlogged after bathing, or when incapacitated by poison, vultures are vulnerable to attack by domestic dogs. Such cases have been recorded (Ashton 1957).

Killed by Gulls

It is likely that large open stretches of water are very difficult for vultures and other terrestrial (i.e. not marine) soaring and gliding birds to cross. In the Mediterranean many large raptors are found washed up on the shores adjacent to the migration routes during the spring and autumn passage (Zu-Aretz & Leshem 1980). On those occasions that inexperienced vultures fly out over the sea, they become vulnerable to opportunistic predators such as gulls (Boshoff 1980).

Fire

Fires at colonies can have a serious effect on eggs and nestlings, and they can presumably be deleterious to free-flying birds as well. Serious fires were noted at the Potberg colony in 1972, 1976 and 1978 (Boshoff & Currie 1981). At the Skeerpoort colony on 26 August 1974, a large fire reduced breeding success on two of the four faces by about 5%, but this could have been 8% if humans had not intervened (Mundy & Ledger 1975).

Mine Fields

War is both good news and bad news for vultures. From time immemorial folklore has held that vultures flock to killing-fields to feed. In modern times, land mines have both generated carcasses for vultures to feed on, and have killed them as they ran along the ground to take off (Mundy 1984: 112).

Summary

Many causes of death have been documented for the Cape Vulture. The next step is to try and estimate the impact of the most important of these and determine how they vary in space and time. Estimates of how five major unnatural mortality have varied in time will be made in the next section. The geographical distribution of birds reported dead from various unnatural mortality factors will be considered in the next chapter.

5.4 The impact of unnatural mortality

What is the impact of unnatural mortality on the population of free-flying Cape Vultures? This question will be considered in terms of temporal trends, colony effects and the spatial location of deaths. The last mentioned effect will be considered below (Chapter Six).

There too many different causes of mortality recorded (Table 5.15) to handle with ease and so they are reduced to five major categories: collision, drowning, electrocution, poisoning and shooting. All other deaths are recorded as unknown. To investigate the temporal effects the numbers of recoveries in each category are tabulated by decade (Table 5.17) from which a number of trends are suggested.

1) The proportion of deaths attributed to unknown causes is decreasing with time.
2) The proportion of deaths reported as collisions is increasing with time
3) Drownings as a cause of death are increasing with time
4) Electrocution was not reported before 1970 but declined from it high point in the 1970s.
5) Other than for a possible peak in the 1960s the proportion of birds shot has remained constant.

It is also hypothesized that the location of the colony at which a nestling was ringed could influence its subsequent fate. It will be shown in the next chapter that there is a concentration of deaths from electrocution in the southwestern Transvaal. Thus birds from the south-central Transvaal and Botswana colonies could be more susceptible to electrocution because their natal colonies are closer. To investigate this cause of death is tabulated against colony (Table 5.18).

Table 5.17
Variation in reported cause of death with time.

Decade	Unknown		Collide		Drown		Electro.		Poison		Shot		
1950s	18	82%	-		1	5%	-		1	5%	2	9%	22
1960s	22	58%	1	3%	4	11%	-		2	5%	9	24%	38
1970s	34	35%	7	7%	8	8%	32	33%	7	7%	8	8%	96
1980s	10	31%	4	13%	9	28%	4	13%	2	6%	3	9%	32
	84		12		22		36		12		22		188

Table 5.18
Variation in reported cause of death with colony of origin.

	Unknown	Collide	Drown	Electro.	Poison	Shot	
Kranzberg	2 100%	-	-	-	-	-	2
Manoutsa	3 60%	-	-	2 40%	-	-	5
Manyana	1 100%	-	-	-	-	-	1
Mannyelanong	6 55%	-	1 9%	2 18%	1 9%	1 9%	11
Skeerpoort	35 45%	5 6%	7 9%	12 16%	8 10%	10 13%	77
Nooitgedacht	-	-	-	-	-	1 100%	1
Roberts' Farm	28 36%	4 6%	7 11%	16 25%	2 3%	7 11%	64
Colleywobbles	6 26%	3 13%	7 30%	4 17%	1 4%	2 9%	23
Potberg	2 67%	-	-	-	-	1 33%	3
Assvogelvlei	1 100%	-	-	-	-	-	1
Column	84	12	22	36	12	22	188

There are only four colonies with reasonable numbers of recoveries: Mannyelanong, Skeerpoort, Roberts' Farm and Colleywobbles. A number of colony effects are suggested for these sites.

1) There is a higher proportion of drownings for birds from Colleywobbles.

3) Electrocutions constitute a higher proportion of deaths for birds from Roberts' Farm.

To investigate these effects a generalized linear model (GLM) was built for each mortality factor (i.e. collision, drowning, electrocution, poisoning and shooting). A binomial model was used in which the number of birds reported dead from a given cause was compared with the total number of birds reported dead from a given colony in a given year. The independent variables were year of death and colony of ringing. All model coefficients are significant at 5%.

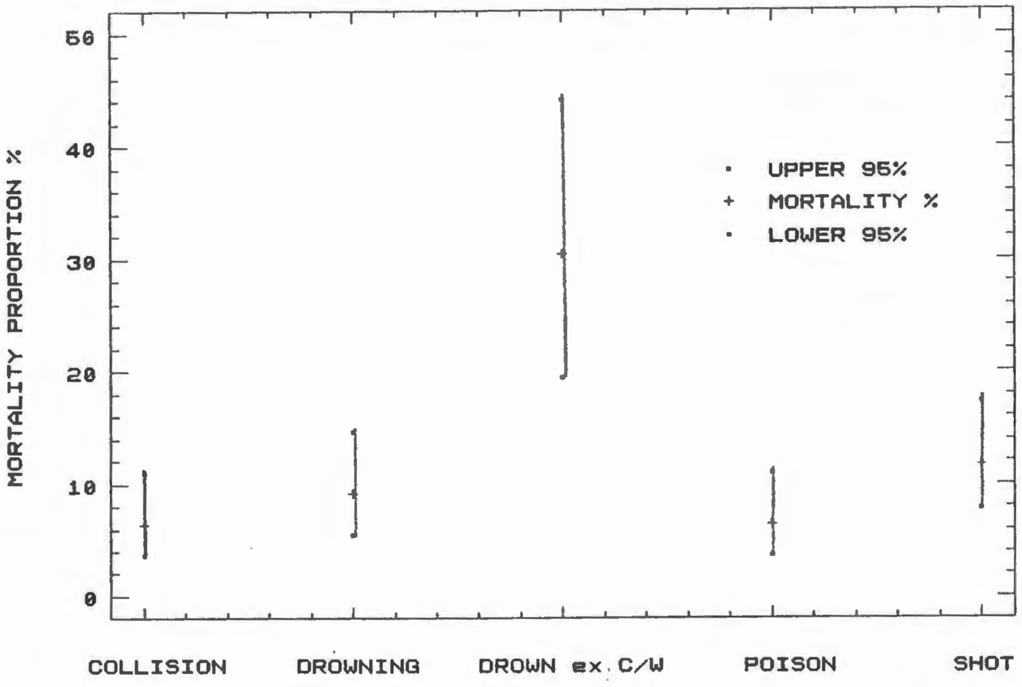

Figure 5.13 Variation in proportion of birds reported dead from a given cause of death.

Table 5.19
Estimated proportion of birds dying from each reported cause of death.

Cause of death	Function	Proportion	Maximum mortality, birds p.a.
Collision	Constant	6.4%	162
Drowning	Constant (not Colleywobbles)	9.1%	230
	Colleywobbles	30.4%	61
Electrocution	Quadratic	See Figure 5.14	25
Poisoning	Constant	6.4%	162
Shot	Constant	11.7%	295

From the GLM models it was found that the proportions of birds dying from collision, poisoning and shooting was constant at 6.4%, 6.4% and 11.7% respectively (Table 5.19). Drowning as a cause of death was the only variable in which the colony of origin was a significant factor: the proportion drowned was 9.1% at all colonies except Colleywobbles where it was 30.43%. Each of these estimates is shown with its confidence limits (Figure 5.13) and it is seen that the estimate of drownings of Colleywobbles' birds is the most variable, it is based on a small sample size (Table 5.18). Why do birds from Colleywobbles suffer more from drowning? Are they visiting areas which hold a particular danger for them?

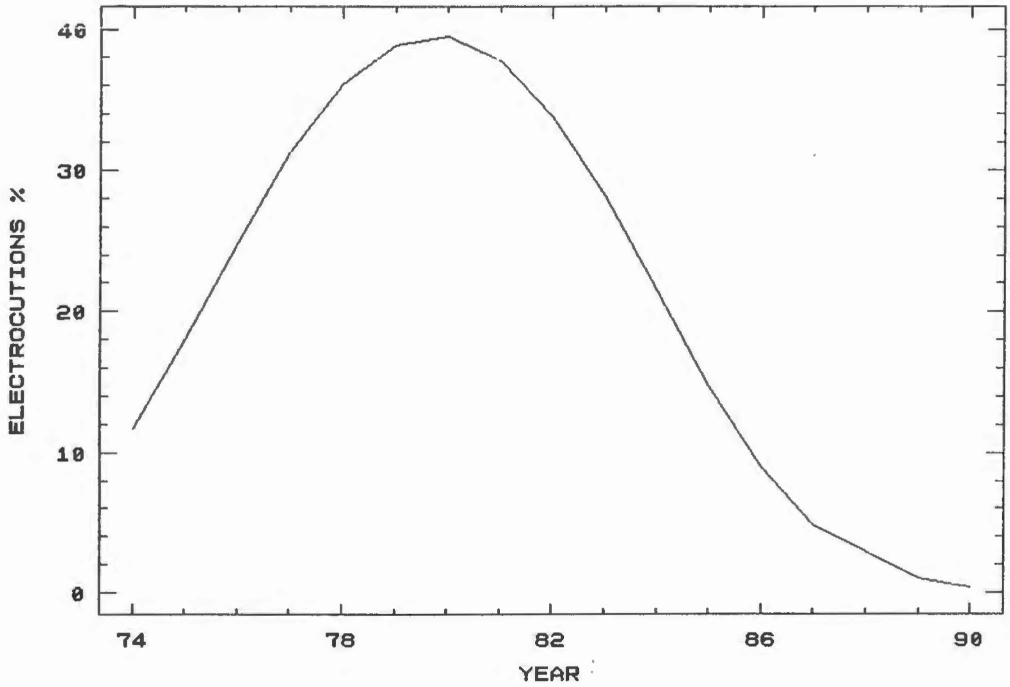

Figure 5.14 Variation in proportion of birds reported dead from electrocution from 1970 onwards.

Electrocution as a cause of death (among birds recovered) was not recorded before 1974 and so the model was fitted to the 1974 - 1989 data only. It was found that the proportion of birds electrocuted was high in the early 1970s but declined strongly through the 1980s (Figure 5.14).

A crude estimate is provided of the maximum number of birds dying from each mortality factor. This is done in the manner described below.

1) The number of breeding pairs is approximately 4400 (Chapter Three).
2) The maximum number of offspring produced per pair p.a. is about 0.6375 (Chapter Four).
3) The proportion entering their sixth year when they are recruited to the adult population is about 10%. Thus about 90% are lost.
4) Thus the annual output of fledglings is 4400*0.6375=2805. Of these 90%, i.e. 2525 will die before reaching adulthood.
5) If it is assumed that probability of a recovery being reported is independent of the cause of death then the proportion of the 2525 deaths p.a. attributable to collision with manmade structures, say, will be 6.4% of 2525, i.e. 161 p.a.

It is conceded that there too many untenable assumptions in the above analysis, but it does give a crude order-of-magnitude picture of the problem. This suggests where efforts to conserve birds should be directed.

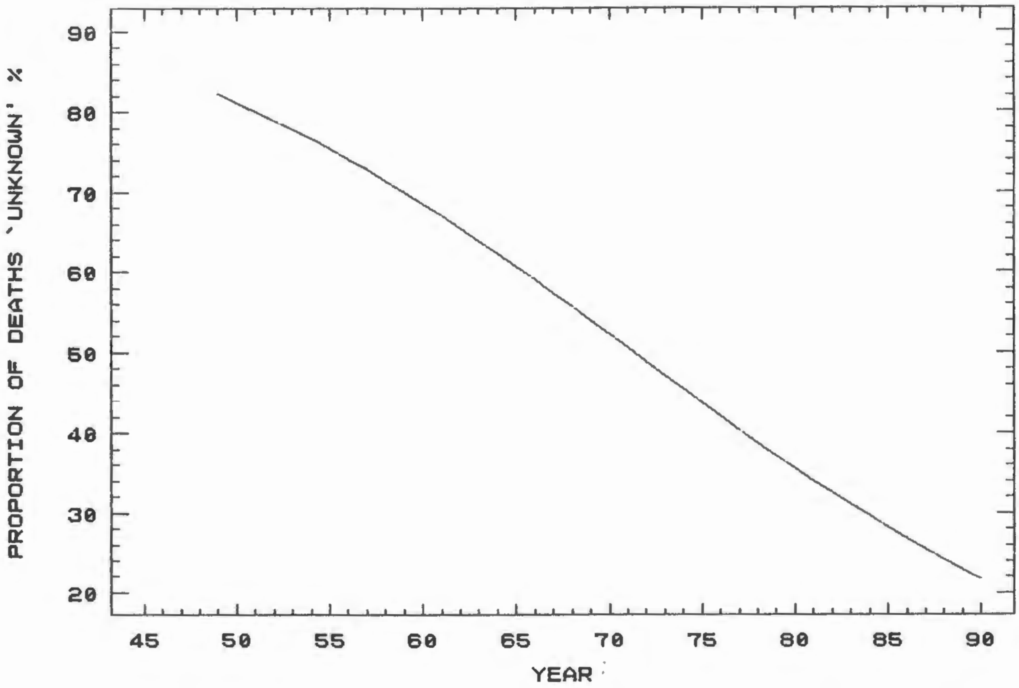

Figure 5.15 Variation in proportion of birds reported dead from unknown causes.

The proportion of deaths attributed to unknown causes is decreasing with time (Figure 5.15). It is possible that this is due to one or more of the following factors.

1) In the early 1970s the Vulture Study Group was formed and its members began searching the screes below colonies for dead birds. They took care with the examination of the carcasses and this led to an improvement in the assessment of cause of death. Their activities also made the land-owners and local residents more conscious of the need for better reporting (pers. obs.).
2) In the mid-1970s the Bird Ringing Unit was put on a permanent footing at the University of Cape Town and the succession of Ringing Officers made a conscientious effort to trace all recoveries and to write to reporters to clarify details (C.C.H. Elliot, T.B. Oatley & C.J. Vernon pers. comm.).
3) In the early 1980s the Vulture Study Group set up a records department and nearly all recoveries were followed up questionnaire which often elicited the cause of death (R. Lindeque, pers. comm.).

The most important result to come out of this analysis is that only electrocution is decreasing as a cause of dead - all other factors are not changing. Thus strenuous conservation measures need to be directed at preventing collisions with manmade structures, drowning in farmers' dams, wanton poisoning and direct persecution.

5.5 Summary

A major aim of this chapter is to provide estimates of survival for each age-class as well as estimates of recruitment. From earlier studies estimates of first-year survival were 17%, 19% and 28.6% p.a. while adult survival was estimated at 71.4% and 74% p.a. Estimates of recruitment were 7.7% and 8.3%. From a review of the literature (mainly of large scavenging birds) it would seem reasonable to expect adult survival to be about 90% to 95% p.a. From comparative studies it is predicted that Cape Vultures should have a longevity of about 25 years in the wild. The oldest known-age Cape Vulture so far monitored is 14 years.

Because it is not possible to identify individual Cape Vultures in the field two marking techniques have been investigated. Initially aluminium butt-rings were fitted, from 1948 to 1969 during which time 3198 nestlings were ringed. From 1970 onwards harder monel metal rings were fitted, 4091 in total to the early 1990s. In addition from 1973 individual (i.e. unique) combinations of colour rings were also attached to many nestlings. Over 3000 nestings were fitted with colour-rings during the 11 year period 1973 to 1983. The resighting of a colour-combination and the finding and reporting of a dead ringed bird are used to estimate age-specific survival.

A detailed analysis of the ring-recovery-reporting process was undertaken to gain insight into the likely biases inherent in the system. It was found that there were reporting rate differences within the following groups.

1) Ring prefix. There was considerable variation in reporting rate between the different ring prefix series used.
2) Metal type. Monel metal rings were reported at a rate twice that of aluminium rings.
3) Colony of ringing. Some colonies surrounded by subsistence farming communities had lower reporting rates than others surrounded by commercial farming communities.
4) Colour-rings. Recoveries with colour rings were much more likely to be reported.
5) Epoch. Reporting rate has increased steadily from the 1950s through to the mid-1980s.

All of the factors investigated interact with each other and so a single multivariate model was fitted. It was found that a model including a colour-ring factor and a cubic temporal trend provided a parsimonious and statistically adequate model of reporting rate.

In view of the stricture of Brownie, Anderson, Burnham & Robson (1985) the ringing-recovery data were not subjected to a detailed statistical analysis (see p. 236 above). This was because it was felt that these data did not meet the most important assumptions of most analytical methods. However, a simple analysis yielded an estimate of first-year survival of

42% p.a., an estimate of 68% p.a. for adult survival and an estimate of 8.1% for recruitment. The great increase in the estimate of first-year survival is thought to be a reflection of the use of better quality rings since 1970.

Since the completion of these researches new models have been developed for the analysis of ring-recovery data (BTJ Morgan, pers. comm.) and it is likely that these new models will permit a more comprehensive analysis of this data-set.

The consistent ringing programme (including colour-rings) in the southwestern Cape since the mid-1970s coupled with an intensive resighting programme since the late 1970s has led to the accumulation of a useful data-set. These data were subjected to analysis and it was found that survival varied both with age and calendar year. One of the models yielded estimates of first-year survival of 46.3% p.a. (95% limits: 36%-57% p.a.). Survival of birds 2+ years was put at 75.4% p.a. (63%-84% p.a.). It was also found that 1983 and 1985 were better than average years for Cape Vultures in the southwestern Cape.

From an examination of the literature and an analysis of the reported cause of death for recovered ringed birds it was suggested that the most important sources of unnatural mortality for Cape Vultures may be gathered into five categories.

1) Collision with manmade objects. It is estimated that 6.4% of all mortalities are due to this factor and that it claims approximately 162 birds p.a.
2) Drowning. Approximately 9.1% of Cape Vulture deaths are due to drowning which claims about 230 lives p.a.
3) Electrocution. A major factor in the 1970s through to the 1980s rising up to 40% of all deaths this factor now seems to be under control and may cause, at most 25 deaths p.a.
4) Poisoning. Both intentional and unintentional poisonings make up about 6.4% of all deaths with up to about 162 deaths p.a.
5) Shooting. This category includes all forms of persecution and makes up the largest category at 11.7% of all deaths causing about 295 deaths p.a.

The number of Cape Vultures reported dead due to unknown causes has steadily decreased with time and it is suggested that this is a consequence of a better informed public, an improved ring-reporting process and more aggressive follow up by the Vulture Study Group.

Estimates of age-specific survival for the Cape Vulture are better now than they ever have been. Unfortunately, they are still woefully inadequate as will be seen below in the chapter devoted to modelling (Chapter Seven).