

Bird Study



ISSN: 0006-3657 (Print) 1944-6705 (Online) Journal homepage: http://www.tandfonline.com/loi/tbis20

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To cite this article: Steven E. Piper, André F. Boshoff & H. Ann Scott (1999) Modelling survival rates in the Cape Griffon Gyps coprotheres, with emphasis on the effects of supplementary feeding, Bird Study, 46:sup1, S230-S238, DOI: 10.1080/00063659909477249

To link to this article: https://doi.org/10.1080/00063659909477249



Published online: 25 Jun 2009.



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Modelling survival rates in the Cape Griffon *Gyps coprotheres,* with emphasis on the effects of supplementary feeding

STEVEN E. PIPER^{1*}, ANDRÉ F. BOSHOFF² and H. ANN SCOTT³ ¹Department of Zoology & Entomology, University of Natal, Private Bag X01 Scottsville Pietermaritzburg, 3209 KwaZulu-Natal, South Africa, ²Terrestrial Ecology Research Unit, Department of Zoology, University of Port Elizabeth, PO Box 1600, Port Elizabeth 6000, Eastern Cape, South Africa and ³PO Box 439, Gansbaai 7220, Western Cape, South Africa

Survival rates are crucial demographic parameters for modelling the population dynamics of the Cape Griffon vulture. Previous survival estimates based on ring recoveries are seriously flawed and have been heavily criticized. To provide better estimates, 97 nestlings were individually colour-ringed in the winterrainfall region of South Africa from 1979 to 1987 and an intensive resighting campaign was mounted for 17.5 years (1980 to mid-1997). Although survival rate is known to vary with age, particularly in the first few years of life, this study indicates that it is also a function of calendar year. Supplementary food was provided for the study population from 1984 onwards and there was a concomitant increase in the survival rate of first-year birds. Eighty generalized linear models were built to estimate survival rate as a function of age, calendar year, cohort and supplementary feeding. First-year survival rate was estimated as 42.3% per annum (95% limits: 29–56%), increasing to 68.9% (54–81%) after the introduction of supplementary feeding. Age-specific survival rates were 88.8% per annum (77–95%) in the second year, 78.7% (64–88%) in the third year and 67.6% (58–76%) for birds aged four years or more. Our survival estimates are higher than previous values and have greater reliability because they are based on direct observations of known-age birds. The loss of colourrings is a serious impediment to estimating survival among older birds and the technique described here was not used to estimate adult survival.

The Cape Griffon is one of the largest vultures in southern Africa and is widely distributed across the subcontinent.¹ There are approximately 4400 breeding pairs in a population of about 12 000 individuals.² Birds take about six years to reach their final adult plumage³ and few individuals breed before then. Pairs do not breed every year and when they do they produce at most one large fledg-ling (twins are very rare). They can occasionally re-lay if the breeding attempt fails early in the season range.¹

*Correspondence author. Email: PiperS@zoology.unp.ac.za

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The Cape Griffon has been the subject of much research and conservation concern over the last 25 years as the population is thought to be in decline.² The Vulture Study Group devised a seven-point plan for the conservation of the Cape Griffon based on the integrated management strategy devised by Plunkett⁴ which includes population modelling and population monitoring.¹ To construct a simple demographic model it is necessary to have estimates of the population size, age-structure and rates at which new individuals are added to the population (i.e. births and immigration) and lost from the population (i.e. deaths and emigration).⁵ Reasonable estimates of fecundity have been produced.² However, difficulties were experienced in providing accurate estimates of the survival rate;⁶ the overall aim of this paper is to make good that deficit.

Analysis of ring recoveries is not an appropriate technique for estimating the survival rate of this species.^{7,8} An alternative to estimating survival from ring recoveries is to use resightings of uniquely colour-ringed birds; in this way survival may be monitored directly, provided all emigration is permanent. If all surviving birds are seen and uniquely identified then it is not necessary to use the Cormack– Jolly–Seber (CJS) models. Observations of colour-ringed Cape Griffons in the winterrainfall region of South Africa were used to estimate survival rates. This deme (i.e. isolated population) is particularly suitable for such an analysis for the following reasons.

1 The population is functionally isolated from the rest of the Cape Griffon population in southern Africa, i.e. there is almost no immigration into, or emigration from, the region; the deme may be assumed to be closed.^{2,9}

2 The population is small (< 90 individuals), has been declining very slowly (about 1% per annum) over the last 40 years and although it is not exactly constant, it is almost so, especially from the mid-1970s.^{2,10-12}

3 Good observations of marked birds have been made at the colonies and roosts in the region from the early 1950s.

A crude population model based on the early estimates of survival showed that the overall growth rate of the population was sensitive to the survival of birds in their first year. Consequently, a trial feeding programme was introduced in 1983 and was fully operational by early 1984. It was designed to provide food to assist first-year birds through their initial year as free-flying individuals, independent of their parents.¹⁰

Large nestlings were ringed each year just prior to fledging. We investigated four factors that could influence their subsequent survival from one year to the next.

1 Age. Many large birds take a number of years to reach adult plumage and their survival rate increases with age. In particular, this has been shown for the congeneric Eurasian Griffon *Gyps f. fulvus*.¹³

2 Calendar year. Many studies of birds have

shown that survival varies from one calendar year to the next.¹⁴

3 *Cohort.* While we have no direct evidence that the nestlings ringed in a particular year are prone to suffer higher or lower mortality than those ringed in other years, we tested for this factor in our models.

4 *Supplementary feeding.* We suspect that the survival of fledglings is lower in this deme than elsewhere in the population and that the provision of supplementary food will increase it. The population is effectively closed (see above) and consequently juveniles seldom escape from the realm dominated by the adults, and lose out in competition for the available food. Older birds are dominant over younger birds at carcasses and, in a region where vultures feed on small carcasses (i.e. domestic sheep), the subordinate birds are less likely to be able to find a meal.¹⁵ Cape Griffon parents will not feed their young unless they are on the nest and will never feed them after the start of the next breeding season.¹

There are two different ways in which these resighting data may be modelled in order to estimate survival: a Cormack–Jolly–Seber (CJS) model or a generalized linear model (GLM).¹⁶ We chose to use the latter as we did not have access to software or expertise but were able to formulate a GLM, which is functionally equivalent.¹⁶

In using resighting data in our GLM, we assume that there are no losses (other than to death) from the colour-ringed population and that if a bird survives to the end of a calendar year it will be seen in a subsequent year. (This is equivalent to assuming that the resighting probability is unity.) There are two potential sources of apparent loss: permanent emigration and the loss of colour-rings. Both these effects will cause our estimates to be negatively biased as will a resighting probability of less than unity.

This paper estimates the survival rates of various segments of the population and determines whether first-year survival increased after supplementary food was supplied.

METHODS

Study area

Cape Griffon nestlings were ringed at two colonies in the Western Cape Province of South

Africa, Potberg $(34^{\circ}22'S, 20^{\circ}33'E)$ and Aasvogelvlei $(33^{\circ}52'S, 21^{\circ}38'E)$, which are about 120 km apart. The Potberg colony¹⁵ is just northeast of Cape Agulhas, the southernmost point on the African continent.

Field methods

From 1952 to 1973 only a standard numbered monel ring was fitted to each nestling, but from 1974 until 1988 nearly all the nestlings were also fitted with a unique permutation of colour rings. Only ringing data from 1979 to 1987 and resighting data from the start of 1980 to mid-1997 are used. While irregular observations of colourringed birds were made 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.17 Members of the Provincial Nature Conservation Agency continued observations of the vultures when this study ended. After a conservation plan was drawn up,10 regular observations were made part of the work-plan of the local conservation staff.

A summary of the years in which each colour-ringed bird was ringed and last seen was compiled for the period 1979 to mid-1997. From this summary, an abstract was constructed giving the number of birds, in each age-class, alive at the start of each calendar year as well as the number which survived until the start of the next calendar year.

Models

The nestlings are ringed in about October, make their first flight in about November or December and fledge in January of the next year.¹⁷ Thus each age-class and cohort corresponds to a calendar year. Let S_{ijk} be the probability that an individual aged i - 1 years at the start of the *j*th calendar year and in the *k*th cohort will survive until the start of the next calendar year when it will be *i* years old. Let there be N_{ijk} individuals, aged i - 1 years alive at the start of the year of which n_{ijk} survive to be alive exactly a year later. If it is assumed that all individuals have the same survival rate, then the appropriate probability distribution is the binomial.¹⁸

The survival rate may be estimated using a GLM. The response variable is modelled with

binomial errors and a logit link function.¹⁹ The logit transform for a binomial response is as shown below.

logit
$$(S_{ijk}) = \ln (S_{ijk} / \{1 - S_{ijk}\})$$

= $F_1 + F_2 \dots + G_1 + G_2 + \dots$
+ $H_1 + H_2 + \dots$ SF

where F_i is age-specific factor for the *i*th age class, G_j is year-specific factor for the *j*th year class, H_k is cohort-specific factor for the *k*th cohort and SF is the effect of supplementary feeding on first-year survival.

The reverse transformation is:

$$S_{iik} = \exp(F_1 + F_2... + G_1 + G_2... + H_1 + H_2 + ... + SF) / (1 + \exp(F_1 + F_2... + G_1 + G_2... + H_1 + H_2 + ... + SF))$$

Thus the values of the response variable are calculated for the numbers alive at the start and end of each year for each cohort (i.e. one value for each row of Appendix 1). This simple approach, compared with the more complex formulation of Cormack,¹⁶ is only possible because we were able to assume that the resighting probability was unity.

All modelling was performed with GENSTAT 5 Release 3²⁰ using the MODEL and FIT directives. The estimates and statistics listed below were provided.

1 The estimates of the parameters (i.e. $F_1, F_2...$), their standard errors and Student's *t*-values.

2 The number of outliers and influential points. (An outlier is a point estimate which is so far from its observed value as to be worthy of comment while an influential point contributes excessively to the GLM).

3 The deviance and degrees of freedom of the fitted model. Note that the deviance is twice the log-likelihood.

4 The predicted values and standardized residuals.

The deviance is asymptotically distributed as the χ^2 distribution, under the null hypothesis, but this approximation is not always a reliable tool for evaluating the goodness-of-fit.¹⁹ The observed numbers of colour-ringed birds surviving (n_{ijk}) were compared with the predicted numbers using the χ^2 statistic. In addition, each GLM with K variables in it was compared with the 'null' model (i.e. a constant survival) because the difference in deviances is known to be approximated better by the χ^2 distribution with K - 1 degrees of freedom.¹⁹ This is the likelihood-ratio test between the model of interest and the null model. A wide variety of models were fitted and the most parsimonious model was chosen using Akaike's information criterion (AIC).^a

RESULTS

The number of nestlings ringed each year varied from 6 to 15 while the number of resightings per individual bird varied from 1 to 125. The oldest birds to be resighted were at least 12 years old. There were no cases in which a bird not recorded as alive in a particular year was resighted in a subsequent year.

Constant survival: model 1

The simplest estimate of the survival rate is a constant, i.e. independent of age, calendar year, cohort and supplementary feeding. The estimate is 68.8% per annum with approximate 95% confidence limits: 66–71%. This model is not an adequate fit to the data, and there are four outliers and four influential points (model 1, Table 1).

Age-specific survival: models 2 and 3

If it is assumed that the survival rate is a function of age only, then it is possible to fit a model with 12 age-classes; this yields a model which is an improvement on fitting just a constant (model 2, Table 1). By reducing the number of age-classes from 12 to four there is no appreciable change in the AIC. This suggests that model 2 with 12 age-classes has too many parameters; four will do just as well (models 2 and 3, Table 1). The number of outliers stays the same but the number of influential points rises from nil to ten (Table 1).

Cohort-specific survival

A number of models were tested and it was found that no one cohort, or selection of cohorts, reduced the AIC (results not shown).

Models 1 2 3 4 5 6 Variables in the model Constant + Age (12 classes) + Age (4 classes) Age (4 classes) + food supplement + Age (4 classes) + food supplement + 5 calendar years + Age (4 classes) + food supplement + 3 calendar years + 10 8 Parameters, K 1 12 4 5 98.2 71.6 91.1 Deviance 127.8 88.3 105.2 74 63 71 70 65 67 Degrees of freedom 3 3 1 3 Outliers 4 3 9 4 10 10 6 Influential points 32.8 25.7 27.424.3 19.4 22.1 Goodness-of-fit, χ² > 0.99 > 0.99 > 0.99 > 0.99 > 0.99 > 0.99 Significance, P 92.5 89.3 82.2 86.2 R^{2} (%) 83.7 129.8 112.3 113.2 108.2 91.6 107.1 AIC

Table 1. A comparison of models fitted.

Effect of supplementary feeding: model 4

The effect of supplementary feeding on the survival of birds in their first year was tested by splitting the first-year birds into two groups: those ringed prior to 1984 and those ringed from 1984 onwards (model 4, Table 1). This model shows a lower AIC value, indicating that supplementary feeding did make a difference. The fit of the model is excellent, but there are three outliers and ten influential points (model 4, Table 1). The three outliers relate to three cohorts (1984, 1986 and 1987) which all died out faster than expected (in 1989, 1991 and 1991 respectively; Table 3). Eight of the ten influential points relate to the survival of birds in their first year and all but one of the first-year cohorts (1980 which is the smallest) are

included. The other two influential points are in 1985. The fitted model, in logit-form, is:

logit $(S_{ij}) = -0.310 (\pm 0.281)$ for first-year birds, no supplementary feeding +0.795 (± 0.322) for first-year birds, with supplementary feeding +2.058 (± 0.429) for second-year birds +1.308 (± 0.356) for third-year birds +0.733 (± 0.200) for birds four-years and older.

Estimates of the age-specific survival rates as a function of supplementary feeding were computed using the inverse transform (Table 2).

Calendar years: models 5 and 6

To test the effects of calendar years, a series of models was constructed by adding calendar years to model 4. Calendar years were added one at a time, two at a time, three at a time etc. and the resulting models evaluated. The best model had five calendar years and had the lowest AIC of all models, with one outlier and six influential points (model 5, Table 1). However, two of the calendar years in the model (1991 and 1994) were based on very few birds at risk (Table 3) and the associated parameter estimates were thus very sensitive to small variations in the data. Thus these two years were removed.

This left a model with three calendar years (1986, 1987 and 1989). The fit of the model is excellent, with three outliers and nine influential points (model 6, Table 1). The three outliers are exactly the same as for model 4. However, only four of the first-year age classes are influential points, compared with eight for model 4, but they are the larger samples. There are three influential points each for 1986 and 1987; these are the largest samples in each year and relate to two of the three temporal variables in model 6 (Table 3). The fitted model, in logit-form, is:

 $\begin{array}{l} \text{logit} \ (\text{S}_{ij}) = -0.310 \ (\pm 0.281) \ \text{for first-year birds,} \\ & \text{no supplementary feeding} \\ +1.258 \ (\pm 0.380) \ \text{for first-year birds,} \\ & \textit{with supplementary feeding} \\ +2.403 \ (\pm 0.460) \ \text{for second-year} \\ & \text{birds} \end{array}$

Table 2.	Estimates	of age-sp	pecific su	rvival r	ates and	l their 9	5% conf	idence	limits fo	or the fi	inal two	models.

		Model 6								
Age-class	Model 4	Other years	1986	1987	1989					
First year, no food supplement	42.3	42.3	_	_	_					
	(29-56)	(29-56)	-							
First year, with food supplement	68.9	77.9	58.6	62.9						
	(54-81)	(62-88)	(23-87)	(26-89)						
Second year	88.7	91.7	81.7	84.2	_					
	(77–95)	(82-97)	(44–96)	(44–97)						
Third year	78.7	84.0	67.9	71.7	74.8					
	(64-88)	(71-92)	(26-93)	(54-85)	(33-95)					
Birds aged ≥4 years	67.5	73.6	52.9	57.3	61.2					
	(58–76)	(63–82)	(41–65)	(45–69)	(49–72)					

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'79	'80	'81	'82	'83	'84	'85	'86	'87	'88	'89	'90	'91	'92	'93	<i>'</i> 94	<i>'</i> 95
9	2	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0
P	<u>3.8</u>	1.8	1.6	0.7	0.7	0.7	-	-	-	-		-	-	-	-	-
§	3.8	1.8	1.7	0.7	0.7	0.7	-	-	-	_	-	_	-	-	-	_
	6	2	2	2	2	1	1	1	1	0	0	0	0	0	0	0
	P	2.5	1.8	1.6	1.4	1.4	0.7	0.7	0.7	0.7	-	-	-	_	_	-
	§	2.5	1.8	1.7	1.5	1.5	0.7	0.5	0.6	0.7	-	-			-	-
		13	6	6	5	3	3	1	1	1	1	1	1	0	0	0
		P	<u>5.5</u>	5.3	4.7	3.4	2.0	2.0	0.7	0.7	0.7	0.7	0.7	0.7	—	-
		§	5.5	5.5	5.0	3.7	2.2	1.6	0.6	0.7	0.6	0.7	0.7	0.7	_	-
			15	7	7	7	5	2	1	1	1	0	0	0	0	0
			P	<u>6.3</u>	6.2	5.5	4.7	3.4	1.3	0.7	0.7	0.7		-	_	-
			§	<u>6.3</u>	6.4	5.9	5.2	2.6	1.1	0.7	0.6	0.7	-	_	_	-
				9	5	4	4	3	3	3	2	1	1	1	1	0
				P	<u>3.8</u>	4.4	3.1	2.7	2.0	2.0	2.0	1.4	0.7	0.7	0.7	0.7
				§	3.8	4.6	3.4	2.1	1.7	2.2	1.8	1.5	0.7	0.7	0.7	0.7
					10	8	7	5	3	3	0	0	0	0	0	0
					P	<u>6.9</u>	7.1	5.5	3.4	2.0	2.0*	-	_	_	-	-
					§	7.8	7.3	<u>4.8</u>	2.9	2.2	1.8*	_	_	-	-	-
						12	10	8	4	4	3	3	2	2	1	0
						P	<u>8.3</u>	<u>8.9</u>	<u>6.3</u>	2.7	2.7	2.0	2.0	1.4	1.4	0.7
						§	<u>9.3</u>	<u>8.2</u>	<u>5.7</u>	2.9	2.4	2.2	2.2	1.5	1.5	0.7
							14	8	7	6	4	4	0	0	0	0
							P	<u>9.6</u>	7.1	5.5	4.1	2.7	2.7*	-	-	-
							§	<u>8.2</u>	<u>6.7</u>	5.9	<u>3.7</u>	2.9	2.9*	-	-	-
								9	5	4	3	3	0	0	0	0
								I	<u>6.2</u>	4.4	3.1	2.0	2.0*	-	-	-
								§	<u>5.7</u>	4.6	3.0	2.2	2.2*	-	-	-

 Table 3. Comparison of the number known to be alive each year with the expected number from models 4 and 6.

I: Expected values for model 4. §: Expected values for model 6. *An outlier. Underline: an influential point.

- +1.659 (±0.391) for third-year birds +1.025 (±0.242) for birds four-years and older -0.910 (±0.390) during the 1986
- calendar year
- -0.731 (±0.417) during the 1987
- calendar year -0.571 (±0.499) during the 1989 calendar year.

Estimates for the age-specific survival rates as a function of supplementary feeding and calendar year were computed using the inverse transform (Table 2).

A comparison of the expected values for models 4 and 6 revealed 19 points, about a third of the data values, for which the difference is greater than 0.3 (an arbitrary measure of a 'real difference'). The expected values from model 4 are bigger than the corresponding values from model 6 for 1986 and 1987, as would be expected from the large negative effect both these years have in the model.

DISCUSSION

Using resightings of colour-ringed birds we were able to produce usable estimates of survival rates, at least for the first three ageclasses. The survival rate of first-year birds showed a statistically significant increase from 42% to 69% after the introduction of supplementary feeding (Table 2).

The earliest estimates of survival of the Cape Griffon, in fact of any vulture of the genus *Gyps*, were computed by Houston²¹ who provided two values: $55 \pm 16\%$ and $44 \pm 5.6\%$ depending on whether the population was assumed to be open or closed. These estimates were criticized⁶ as being far too low and for making the unwar-

ranted assumption that survival is constant across all age-classes. Our estimate of constant survival rate (model 1, Table 1) is 68.8%, which is 25% higher than that of Houston.²¹

Using a much larger data set of ring-recoveries than that used by Houston,²¹ Piper et al.⁶ estimated survival rates at 17%, 61%, 74% for the first three age-classes. It was shown subsequently that the reporting rate varied among the age-classes and that the methods of analysis were flawed, leading in turn to an underestimate of survival for the first age-class. If we ignore the effects of supplementary feeding, our estimates for the first three age-classes are 55%, 89% and 79%, respectively (model 3, Table 1), markedly higher than the previous ones. In a parallel study of the Eurasian Griffon Gyps f. fulvus in France,13 the estimated survival rate of age-classes one to three was 85.8% (76–92%), which is higher than our average of 74%. However, they studied a newly introduced population that was provided with supplementary food, is estimated to have three times more food than necessary and is growing.

The estimates produced here (Table 2) have greater reliability than those based on an analysis of ring-recovery data for the following reasons.

1 The data used to estimate survival come from resightings only, no data from recaptures or recoveries are used. This removed the very many biases associated with trap-shy/traphappy birds and with the process of reporting dead birds.⁸ We believe that all the marked birds in the deme were seen every year, and hence there was no variation in re-encounter rates to contend with (cf Sarrazin *et al.*¹³ who had to model the resighting rate which was less than complete in some years).

2 Continuous monitoring of all known-aged birds on a yearly basis means that it is possible to separate out many age-specific, cohortspecific, calendar-year-specific and other competing causes of variation in survival. However, the data matrix has only 75 cells (Appendix) which limits the maximum degrees of freedom the model may possess.

While the use of resightings of colour-ringed birds has advantages the following practical issues have to be taken into account.

1 The process of observing colour-ringed birds is time-consuming and expensive. It is possible to sit in a hide and watch a carcass for two or

more days without a single bird coming down to feed and then, when they do, the action is so fast and furious that many colour-ring sets are not observed in their entirety. The observations need to be undertaken throughout the geographical range occupied by the deme sufficiently often during the year to be certain that all the living, marked birds are seen.

2 As the study progressed, it became clear that birds were losing colour-rings. In some cases, even with the loss of one or two rings, it was still possible to infer the exact identity and age of an individual by making use of additional cues such as plumage. In some cases it was not possible to be certain of a bird's identity but it was possible to allocate it to a particular cohort. In both such cases it was still possible to include the bird in the analyses. However, there are now birds in this deme with partial colour-ring sets. Although these birds are still alive they are treated as lost to the estimation process.

3 We have no way of knowing how many birds are still alive but living outside the deme; these are treated as lost in the survival-estimation process.

Thus birds can be lost from our enumeration process in three ways: death, permanent emigration and colour-ring loss. The consequence of this is that our estimates of survival rate are negatively biased. However, birds lost from a deme through permanent emigration are both a demographic and genetic loss because they no longer contribute to the future of the deme. Thus our estimate of survival is biased numerically but not in terms of its biological consequences. Because ring-loss is a cumulative process, the negative bias in our estimates increases with the birds' age. We suggest that the decreasing estimates of survival with age from the third age-class onwards (Table 2) are artefacts of progressive ring-loss. Hence we did not attempt to provide estimates of the survival rates of adult birds.

In formulating this model we have assumed that the resighting probability is unity or, more specifically, if a bird survives to the end of a calendar year then it will be seen at least once in some subsequent year (which is a slightly weaker assumption). If this is not true then our estimates will be negatively biased, with this bias acting in the same direction as the biases due to ring loss and permanent emigration. In a parallel situation, Cormack¹⁶ opined Although a constant capture probability is equally unbelievable, its assumption can increase the precision of survival estimates, at the cost of increasing bias if the assumption is false.' All the biases in our estimates are in the same direction and so we can conclude that our estimates are minimum values. However, we are not sure of the effects that the violation of the assumption that all live birds are resignted will have on the variance estimates.

In formulating this model, we have assumed that there are no long-term trends in survival and that it is only for the years 1986, 1987 and 1989 that survival rates are lower. We can offer no explanation as to why these were years of lower survival for the vultures. We have not tested for interaction effects between the explanatory variables as the sample sizes are too small and there are no replicates.

The resighting of colour-ringed birds is the only viable way to collect data from which to estimate survival in such a large, free-flying bird. During the entire time that this colony has been studied (1952–97) only a handful of birds have been captured as free-flying birds and even fewer have been recovered. Hence, recaptures and recoveries are likely to contribute very little information.

The estimates derived from the models in this study have indicated the potential value of a supplementary feeding programme in the conservation of this threatened species. This aspect will be dealt with in a separate paper.

ACKNOWLEDGEMENTS

The following persons helped with the collection of data in the field: Dr A.S. Robertson, Mr M. Scott and Nature Conservation Department staff at de Hoop Nature Reserve. Dr T.B. Oatley and the staff of Safring are thanked for their support while many useful comments and valuable criticism was provided on this paper (and the Piper thesis which preceded it) by Drs S.R. Baillie, P.J. Mundy, A.S. Robertson and M. Samuel, Prof. D.S. Butterworth and an anonymous referee.

ENDNOTES

a. Model selection is currently an important topic of research in capture-recapture and

allied studies. Akaike's information criterion (AIC), as well as a number of modifications thereof, have been advocated.²² For GLMS, an analogous model selection criterion is the Q statistic: Q = Deviance + $\alpha K \Phi$ where α and Φ are constants while K is the number of parameters in the model.¹⁹ For binomial models with no over-dispersion a value of Φ = 1 is suggested. The value recommended for α is between 2 and 6. A value of α = 2 was chosen because it makes the Q statistic identical to the AIC.

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