MANAGEMENT OF THE AFRICAN PENGUIN *SPHENISCUS DEMERSUS* – INSIGHTS FROM MODELLING

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SUMMARY

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The African Penguin *Spheniscus demersus* has decreased markedly in numbers through the 20th Century. In the first half of the century its eggs were harvested commercially, probably at a rate of 48% of total eggs produced. In 1910, the number of birds aged two or older at Dassen Island was estimated to be 1.45 million. This decreased to 0.22 million in 1956, 0.14 million in 1967 and just 0.03 million in 1990 – a loss of 98%. A colony may take more than 50 years to recover from a catastrophic oiling event, even with rehabilitation. In the long term, low-level chronic oiling can have a greater impact than a once-off catastrophic event, especially if disturbance results in substantial losses of clutches. The actual disturbance caused in searching for and collecting oiled birds requires further research, and techniques need to be developed to minimize this disturbance. The proportion of first-year birds that survive is probably about 0.5.

INTRODUCTION

The African or Jackass Penguin *Spheniscus demersus* is endemic to southern Africa, where it breeds along the coasts of Namibia and South Africa between Hollams Bird Island to the south of Walvis Bay and Bird Island in Algoa Bay (Shelton *et al.* 1984). It was abundant at the start of the 20th Century. However, the overall population has decreased throughout the 20th Century (Crawford *et al.* 1990, 1995), leading to its classification in South Africa as 'Vulnerable' (Brooke 1984, Ellis *et al.* 1998).

Various factors have contributed to this decrease. In the first half of the 20th Century, commercial exploitation of eggs is thought to have drastically reduced numbers of penguins at some breeding localities, especially at Dassen Island. The last authorised egg collections were made in 1967 (Shelton *et al.* 1984).

At some islands the mining of seabird guano has influenced the quality of nesting habitat. Instead of being able to burrow into the guano, where extremes of climate are ameliorated, most African Penguins must now nest in the open, where they are often subject to heat stress. In addition, they are rendered more susceptible to displacement from breeding areas by larger animals, such as Cape Fur Seals *Arctocephalus pusillus pusillus* (e.g. Crawford *et al.* 1989). In some areas, mining of guano has created depressions leading to flooding of nests.

In the second half of the 20th Century, large-scale purse-seine fisheries developed off Namibia and South Africa, exploiting schooling epipelagic fish that are the main prey of African Penguins. Stocks of some prey were greatly reduced (Crawford & Shelton 1978) and their availability to penguins altered (Crawford 1981). This is thought to have led to a redistribution of the African Penguin population, with severe decreases in numbers in the west being partially offset by increases to the east (Crawford *et al.* 1990).

In the latter part of the 20th Century, African Penguins have also been subject to contamination by oil spilt at sea. Such oiling has been both chronic and catastrophic. The worst incident occurred in 1994, when oil washed ashore at Dassen and Robben Islands affecting about 10 000 penguins (Crawford 1994). Oiling causes mortality, as well as disruption of breeding activities when contaminated birds are removed from their nests for rehabilitation.

As the 21st Century begins, there is renewed economic interest in African Penguins, which have become a major attraction for tourists. Between September 1995 and February 1996, 160 000 people visited Boulders Coastal Park, the majority to view penguins (Morgan 1996).

In this paper, we model the dynamics of African Penguin populations to explore some of the issues related to their management. We have concentrated on the harvesting of eggs, which was the most important factor in the initial decrease of the species, and oiling, a major present concern for which the pros and cons of various management strategies have yet to be quantified.

Particular questions we sought to address were:

1. What level of exploitation would have resulted in the observed decrease of harvests of penguin eggs at Dassen Island through the first part of the 20th Century?
2. Given this level of exploitation, what was the likely population of African Penguins at Dassen Island at the start of the 20th Century?
3. Was the season of egg collecting at Dassen Island optimal, or could the impact of harvests on the population have been lessened by harvesting in a different season?
4. What levels of egg collection at colonies are sustainable under different harvesting strategies?
5. What is the long-term impact on colonies of African Penguins of both chronic and catastrophic oiling?

6. What long-term benefit to colonies might plausibly result from modification of techniques for the capture of oiled penguins?

THE MODEL

The model applied was similar to that used by Crawford *et al.* (1992) to investigate the dynamics of the South African population of Cape Cormorants *Phalacrocorax capensis*. The number of pairs of penguins at a colony that have the potential to breed in year t was computed as:

$$P_t = \sum_{i=2}^{I} \frac{(N_{i,t} * b_i)}{2} \quad ,$$

where:
P_t = the number of pairs at a colony in year t that have the potential to breed,
I = the number of age-classes,
$N_{i,t}$ = the number of birds alive in age-class i in year t,
b_i = the maximum proportion of birds in age-class i that is capable of breeding.

The number of eggs laid was calculated for each quarter of a year (January to March, April to June, July to September and October to December). For any quarter q of year t the number of eggs produced was:

$$\begin{aligned} E_{t,q} = {} & (P_t * A_t * B_q * c) + \\ & (H_{t,q-1} + (E_{t,q-1} - H_{t,q-1}) * CL) * Rc + \\ & (E_{t,q-2} - H_{t,q-2}) * BL * Rb + \\ & (E_{t,q-2} - H_{t,q-2}) * (1-(CL+BL)) * Rs \quad , \end{aligned}$$

where:
$E_{t,q}$ = the number of eggs produced in quarter q of year t, set as zero for q < or = 0,
A_t = the proportion of mature birds that breed in year t,
B_q = the proportion of mature birds that produce their first clutch for year t in quarter q,
c = the number of eggs laid per clutch,
$H_{t,q}$ = the number of eggs harvested in quarter q of year t, set as zero for q < or = 0,
CL = the proportion pairs that lose whole clutches other than as a result of harvesting,
BL = the proportion of pairs that lose broods,
Rc = the proportion of pairs, which lose whole clutches, that relay,
Rb = the proportion of pairs, which lose broods, that relay,
Rs = the proportion of pairs, which successfully fledge one or more chicks, that relay.

Note that:

$$E_t = \sum_{q=1}^{4} E_{t,q} \quad ,$$

that:

$$H_t = \sum_{q=1}^{4} H_{t,q} \quad ,$$

and that:

$$\sum_{q=1}^{4} B_q = 1 \quad .$$

It is assumed that pairs that relay following the loss of clutches produce the new clutch in the quarter following that in which the eggs were lost, but that those that relay following loss of broods or after successfully fledging chicks do so two quarters after that in which their previous clutch was laid. Incubation of clutches lasts about 41 days and replacement clutches are laid on average 45 days after clutch failure (Randall 1989). Chicks fledge at an age of between 61 and 130 days, the average at St Croix Island being about 90 days (Randall 1989).

The overall harvest of eggs in year t (H_t) was computed as a proportion of the total production of eggs (E_t) in the absence of harvesting. Thus:

$$H_t = E_t * Hpn_t \quad ,$$

where Hpn_t = the proportion of the natural production of eggs that is harvested in year t.

The proportion of the harvest that is taken in each of the four quarters ($HQpn_q$) was specified, such that:

$$\sum_{q=1}^{4} HQpn_q = 1 \quad .$$

Then:

$$H_{t,q} = H_t * HQpn_q \quad .$$

The number of chicks fledged in year t is:

$$N_{1,t} = ((\sum_{i=1}^{4} E_t) - H_t) * s_e * s_c \quad ,$$

where $N_{1,t}$ = the number of chicks fledged in year t,
s_e = the proportion of eggs that survive,
s_c = the proportion of chicks that survive.

Apart from eggs and chicks, six age classes of African Penguins were recognised in the model; first-year birds for the approximately six-month period following fledging until the end of the year in which they were hatched (i= 1), second-year birds aged from one to two years (i = 2), third-year birds from two to three years (i = 3), fourth-year birds from three to four years (i = 4), fifth-year birds from four to five years (i = 5), and birds aged five years or older (i = 6). Thus, for this application of the model, I = 6. At the start of each year, numbers of birds alive in the five oldest age classes were computed as follows:

for i = 2 to 5

$$N_{i,t} = N_{i-1,t-1} * s_{i-1} \quad ,$$

where s_i = proportion of birds in age-class i surviving to the end of the year;

for i = 6

$$N_{6,t} = N_{5,t-1} * s_5 + N_{6,t-1} * s_6 \quad .$$

In the model, s_i was assumed the same for i = 2 to 6, but a different value was used for birds in their first year, when mortality is likely to be higher.

The above model does not include density-dependent effects on survival and production. Therefore, it is important that results presented in this paper are viewed as preliminary.

THE PARAMETERS

Mean values of parameters used in the model, and their standard deviations or ranges, were those measured for penguins at Robben Island during 1988–1995, or used in a model of the population dynamics of penguins at this island (Crawford *et al.* 1999). The mean proportion of birds in each year class that is capable of breeding, and the associated range, was derived from the two estimates available: at St Croix Island (Randall 1983) and at Robben Island (Crawford *et al.* 1999). Parameter values are listed in Table 1.

Juvenile survival (s_1) was calculated so as to maintain the population in equilibrium in the absence of harvesting, i.e. $N_{i,t+1} = N_{i,t}$ all i. In this procedure, the proportion of birds laying their first clutch of the year in each of the four quarters was assumed fixed. Other parameters were assumed to be Normally distributed about their mean and were allowed to vary within three standard deviations of the mean, the range that includes 99.6% of the values of a Normally distributed parameter. Where the standard deviation was not known, the estimated range for the parameter was assumed to include 99.6% of the values.

To generate s_1, a value of each parameter was selected at random from its distribution. This was accomplished by adding to the mean a component based on its standard deviation. Thus for parameter D:

$$D = \overline{D} + Z_d \quad ,$$

where $\overline{D}$ is the mean value of D and Z_d has a Normal distribution with mean zero and range $-3s_d$ to $+3s_d$, where s_d is the standard deviation of $\overline{D}$. An algorithm described by Atkinson & Pearce (1976) was used to generate random numbers for a standard Normal distribution. These values were transformed to generate the values of Z_d using the appropriate means and standard deviations. All proportions were truncated to fall within the range 0.0 to 1.0.

S_1 was restricted to the range 0.3 to 0.7 (Crawford *et al.* 1999), consistent with field estimates of first-year survival (Randall 1983, La Cock *et al.* 1987, La Cock & Hänel 1987). Sets of parameters estimating s_1 within this range, and the corresponding estimate of s_1, were stored, until 2000 such sets were available.

EGG HARVESTS AND POPULATION SIZE AT DASSEN ISLAND

Records of the numbers of eggs harvested at Dassen Island are available for most years between 1900 and 1967, the last year that eggs were collected at the island (Shelton *et al.* 1984). There were interannual fluctuations in the egg harvest. However, the maximum annual harvest of eggs in any decade decreased steadily after 1910–1919 (Fig. 1), and for this period it was assumed proportional to the breeding population of penguins at the island. A linear regression was fitted to the data to estimate the decadal rate of decrease in the egg harvest, b:

$$H_d = H_0 - b * d \quad ,$$

where H_d = the maximum annual harvest of eggs in decade d: decade 0 = 1910–1919, 1 = 1920–1929 ... 5 = 1960–1969.

The value for b was divided by 10 (converting decades to years) to obtain the estimated annual rate of decrease in the egg harvest.

The model was run for 1910–1967 using an annual time step, with t = 0 representing 1910 and t = 57 representing 1967. It was run over this period for each of the 2000 sets of parameters generated that maintain the penguin population in equilibrium in the absence of harvesting. In each instance, the proportion of the natural production of eggs that was harvested at Dassen Island (H_t) was incremented from 0.00 in steps of 0.01 until the annual rate of decrease in the number of breeding pairs at the island $((P_0–P_{57})/57)$ first exceeded the estimated annual rate of decrease in the egg harvest (b/10).

This value of harvesting rate, together with the parameter set that had estimated it and the y-intercept of the regression of maximum egg harvests per decade against time, was used in the model to estimate the population of adult penguins at t = 0 (1910).

Once the adult population at t = 0 had been established, the model was re-run using the same parameter set to obtain estimates of the population at t = 46 (1956) and t = 57 (1967). The year 1956 was chosen because Rand (1963) estimated the population of penguins at Dassen Island then, based on aerial photographs taken on 23 November. Additionally, the model harvest of eggs was computed annually, enabling comparison with the actual harvest taken.

This procedure was followed for each of the 2000 parameter sets that maintain the penguin population in equilibrium in the absence of harvesting. Thus, 2000 estimates of the harvesting rate (H_t), the adult population in 1910, 1956 and 1967, and the annual egg harvest were generated, enabling means, standard deviations and 2.5 percentile values for these parameters to be calculated.

For most years between 1910 and 1967, the number of eggs collected at Dassen Island was recorded for each month (unpublished records in the possession of Marine and Coastal Management). The average proportion of the annual harvest taken in the first quarter of the year was 0.36, in the second quarter 0.62, in the third quarter 0.02 and in the fourth quarter 0.00. These proportions were used as the values for $HQpn_q$ in estimating the number of breeding pairs of African Penguins at Dassen Island in 1910.

Using a harvest rate of 10% (H_t), the proportions of eggs harvested in the various quarters ($HQpn_q$) were varied to ascertain whether alternative harvesting strategies would have slowed or increased the rate of decrease of the penguin colony.

The distribution of the egg harvest through the year that had the least impact on the colony was then used in the model of the penguin colony at Dassen Island to ascertain whether there exists a harvesting rate that would not have caused the colony to decrease. Again the 2000 parameter sets that would maintain an equilibrium situation were used, and the number of adults at the start was set to equal the mean number modelled for 1910. In each instance, H_t was set initially to zero and then incremented in steps of 0.01 until

$$\sum_{i=2}^{6} \frac{N_{i,57}}{N_{i,0}} < 1.0 \quad .$$

OILING AND RESCUE

Oiling of African Penguins is both catastrophic and chronic. Events up until 1994, in which more than 1000 African Penguins were oiled, are listed by Underhill *et al*. (1999). In November 1948, the *Esso Wheeling* wrecked off the mainland at Quoin Point and a large quantity of oil reached Dyer Island. The Superintendent of the Government Guano Islands wrote 'It is estimated that at least one third of the penguin population died, and that it will take at least half-a-century before the number of birds will be restored to their former strength.' (Kruger 1949, p. 602). This scenario was modelled.

A penguin colony was arbitrarily initiated with a population of 100 000 adults, assigned to age-classes two to six so as to reflect an equilibrium situation, given mean values of the parameters listed in Table 1. The model was run for 10 years, when the number of birds in each of age-classes 3 to 6 was computed and then reduced by a third. The model was run for a further 50 years, in all of which the number of birds aged two or older was computed. The initial 10 years were included to ensure a population of pre-breeders at the time of oiling. In each of the 60 years, each parameter listed in Table 1 and s_1 were selected at random from values occurring in the 2000 derived sets of parameters that would maintain the population in equilibrium. All proportions were truncated to have a value between 0.00 and 1.00. It was assumed that there was no immigration to or emigration from the colony.

In 1994, some 10 000 penguins were oiled following sinking of the *Apollo Sea*. Approximately half died, the remainder being successfully returned to the wild after rehabilitation (Underhill *et al.* 1999). To examine the recovery of a penguin colony given rehabilitation, we repeated the above analysis but returned to the population in year 11 half of the birds removed in year 10, augmenting the age of returned birds by one year.

Rehabilitation of penguins oiled by minor spills, which occur at a chronic level and impact 0.24% of the population annually (Adams 1994), necessitates the continual checking of breeding colonies for the presence of oiled birds, and then their capture, rehabilitation and release. Disturbance to the breeding colony may result both from searching for oiled birds and their subsequent capture. This is most likely to affect birds nesting in the open, as for example at Dyer Island, where most birds breed in dense colonies on the surface.

At Jutten Island, daily passage through a low-density colony of African Penguins over a period of seven days caused loss of eggs to Kelp Gulls *Larus dominicanus* (Hockey & Hallinan 1981). The numbers of adults at nests with eggs or chicks decreased from 37 on day two to 32 on day three and 22 by day seven, the reductions being attributable to predation (Hockey & Hallinan 1981). The decreases amount to 14% between days two and three and about 40% after one week. A 40% loss of clutches was assumed to apply in colonies, such as Dyer Island, that are checked for oiled birds on a daily basis, and 14% was used as a scenario for searches conducted at weekly intervals.

TABLE 1

Means and standard deviations or ranges of parameters used in the model

Parameter	Mean	Standard deviation or assumed range (r)
Clutch size, c	1.857	0.044
Proportion of pairs that lose whole clutches other than as a result of harvesting, CL	0.471	0.117
Proportion of pairs that lose broods, BL	0.288	0.074
Proportion of pairs, which lose whole clutches, that relay, Rc	0.305	0.101
Proportion of pairs, which lose broods, that relay, Rb	0.218	0.153
Proportion of pairs, which successfully fledge one or more chicks, that relay, Rs	0.218	0.114
Proportion of eggs surviving to hatch, S_e	0.548	0.078
Proportion of hatched chicks that fledge, S_c	0.370	0.073
Proportion of birds in age-class i that survive one year, S_i for i=2 to 6	0.86	0.82 – 0.90 r
Proportion of mature birds that breed, A	0.834	0.126
Proportion of birds in age-class i that is mature	i = 1: 0.00	0.00 – 0.00 r
	i = 2: 0.00	0.00 – 0.00 r
	i = 3: 0.05	0.00 – 0.10 r
	i = 4: 0.33	0.33 – 0.33 r
	i = 5: 0.74	0.67 – 0.80 r
	i = 6: 1.00	1.00 – 1.00 r
Proportion of mature birds that produce their first clutch in quarter q, B_q	q = 1: 0.69	
	q = 2: 0.27	
	q = 3: 0.04	
	q = 4: 0.00	

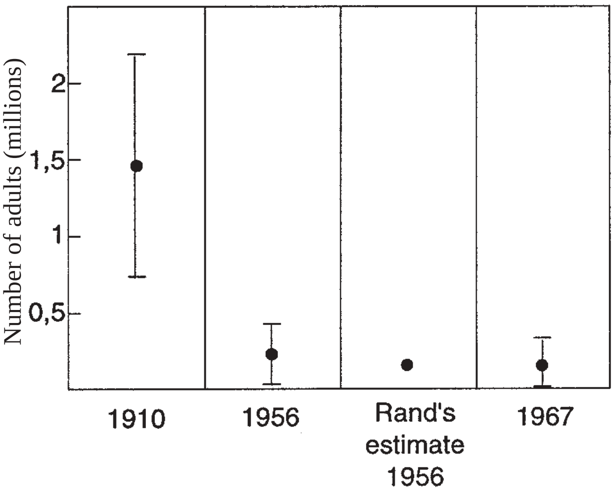

Fig. 1. Maximum annual number of African Penguin eggs harvested per decade at Dassen Island, 1910–1967.

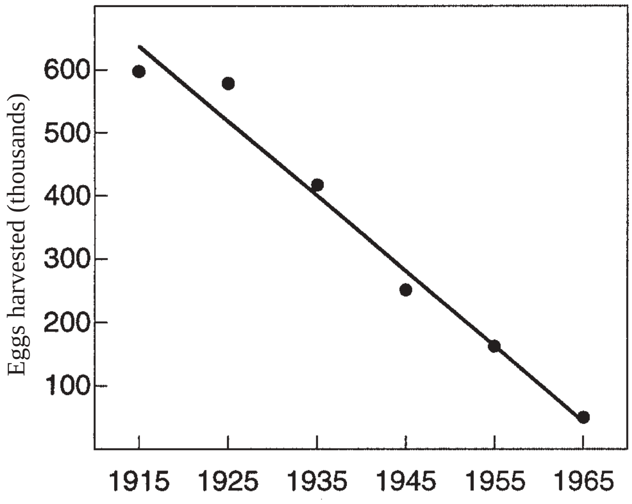

Fig. 2. Plot of the mean model estimates of African Penguin eggs harvested at Dassen Island, against the recorded number of eggs harvested in the middle of each decade.

At Dyer Island, the technique used to capture oiled penguins (a large 'butterfly'-type net is brought down on top of them, often while they are in a group of breeding birds) causes considerable disturbance to nearby breeders (Crawford *et al.* 1995). Mortality of eggs and chicks results as these are taken by Kelp Gulls (R.J.M.C. pers. obs.), but has not been quantified. The losses of clutches of one, two and three neighbouring breeding pairs for every bird caught for cleaning were modelled. Additionally, it was assumed that the clutch or brood belonging to an oiled bird was lost, although an occasion when a partner of a bird caught for rehabilitation successfully raised a brood is known (Underhill *et al.* 1999).

We modelled the effect of chronic, low-level oiling using the same approach as for catastrophic oiling described above. However, instead of reducing the population by one third in year 10, in this and each subsequent year 0.24% of all birds aged two years and older (i.e. i = 3 to 6) was removed from the population. We then modelled seven scenarios:

1. There was no search for oiled birds, which were therefore all presumed to die. It was assumed that only one of a pair was oiled, and that all clutches belonging to a pair of which one bird was oiled were lost. However, there was no loss of other clutches as a result of disturbance.
2. It was assumed that there were daily searches for oiled birds, and that all of these were collected for rehabilitation and release. Rehabilitation success was taken to be 80%, a level that has been attained when the intake of oiled birds is not at catastrophic levels (Crawford 1993), and these birds were all returned to the island in the following year with age incremented by one year. If 80% of the oiled birds were successfully rehabilitated and 0.24% of birds were oiled, then 0.048% of adults died from oiling per year. It was again assumed that only one of a pair was oiled, and that in the year of collection all clutches belonging to a pair of which one bird was oiled were lost. Additionally, it was assumed that for every oiled bird collected three other clutches were lost as a result of disturbance during collection, and that 40 % of all remaining clutches were lost because of disturbance during searches. Oiling was assumed to be equally likely during all quarters of the year, so that the sum of the three clutches lost per oiled bird was modelled in the same manner as harvesting in the previous section, with the proportion of the sum lost per quarter set at 0.25 for all quarters.
3. As for scenario 2. but for each oiled bird collected only two other clutches were lost as a result of disturbance during collection.
4. As for scenario 2. but for each oiled bird collected only one other clutch was lost as a result of disturbance during collection.

5.–7. As for scenarios 2.–4. but assuming searches for oiled birds were only conducted once per week and therefore that the proportion of other clutches lost as a result of disturbance during searches reduced to 14%. The number of birds successfully rehabilitated was reduced from 80% to 70% because of the less frequent nature of searches. If 70% of oiled birds were successfully rehabilitated, 0.072% of adults died from oiling each year.

As in the investigation of catastrophic oiling, the model was run 250 times for each scenario. For each year, the mean and standard deviation of the number of birds aged two and older were computed.

RESULTS

First-year survival

The mean survival rate and standard diviation of first-year birds (6–12 months, s_1), calculated from 2000 parameter sets that would maintain the population in equilibrium, was 0.51±0.11.

Egg harvests at Dassen Island

The mean proportion of eggs harvested that decreased the breeding population at the same rate as the maximum recorded annual harvest of eggs in any decade was 0.65±0.25. This proportion was calculated as a fraction of eggs that would have been produced in the absence of harvesting, i.e. discounting replacement clutches that resulted from harvesting. However, when certain parameter sets were used, the number of eggs required to be collected to achieve the specified level of harvesting exceeded the modelled production of eggs in some

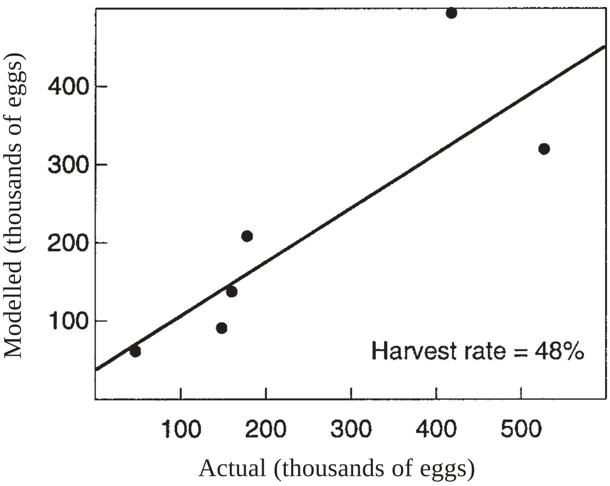

Fig. 3. *Adult population size of African Penguins (aged two and older) at Dassen Island – modelled estimates and Rand's (1963) estimate for 1956. Vertical bars indicate standard deviations about the means (see text for 2.5 percentile values).*

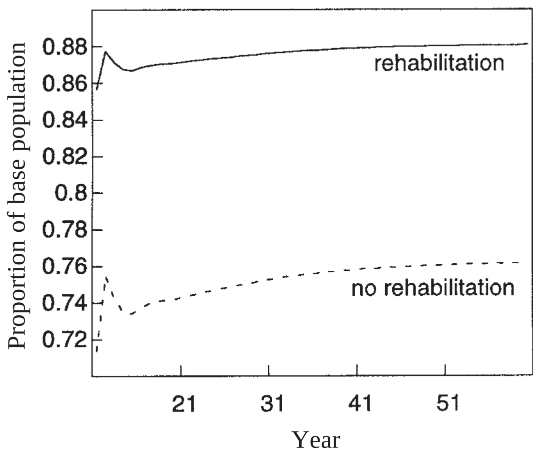

Fig. 4. *Mean model estimates of numbers of African Penguins aged two years and older, for catastrophic oiling events with and without rehabilitation, expressed as a proportion of the mean population that would have existed in the absence of oiling.*

quarters of the year. The mean harvest proportion of all eggs produced, in this case including clutches replaced when eggs were harvested, that best fitted the presumed decrease in penguin numbers was 0.48$\pm$0.09, median = 0.47. The modelled decrease in egg harvests produced by this latter estimate matched the recorded decrease in egg harvests at Dassen Island (Fig. 2).

Population size at Dassen Island

The mean number of birds aged two years and older estimated to be at Dassen Island at *t* = 0 (1910) was 1.45 million (median = 1.30 million), with upper and lower 2.5 percentiles 3.13 and 0.51 million respectively (Fig. 3). The mean breeding population was 0.57 million pairs (median = 0.52 million; upper and lower 2.5 percentiles = 1.20 and 0.21 million, respectively). At *t* = 46 (1956), these values had respectively decreased to a mean of 0.22 million birds (median = 0.19 million; upper 2.5 percentile = 0.45 million; lower 2.5 percentile = 0.08) and 0.09 million pairs (median = 0.08 million; upper 2.5 percentile = 0.19; lower 2.5 percentile = 0.04 million). At *t* = 57 (1967), the last year that a harvest of eggs at Dassen Island was recorded, numbers had decreased to a mean of 0.14 million birds (median = 0.12 million; upper 2.5 percentile = 0.30 million; lower 2.5 percentile = 0.05 million) and 0.06 million pairs (median = 0.05 million; upper 2.5 percentile = 0.12 million; lower 2.5 percentile = 0.02 million). Therefore, by 1967 the estimated number of birds aged two or older had decreased to less than 10% of the level in 1910 (Fig. 3).

Season of egg harvests

Given a harvest rate (H_t) of 10%, the model was relatively insensitive to the choice of harvesting season. Population sizes after 57 years, expressed as a proportion of those at the start, ranged from 0.63 to 0.66 for birds aged two and older, and 0.64 to 0.67 for breeding pairs. The highest mean numbers of adults and breeders after 57 years resulted when as much as possible of the egg harvest was taken in the third quarter, and the balance in the first quarter. The lowest numbers after 57 years were recorded when 90% or more of the egg harvest was taken during the first and second quarters. High harvest proportions taken in the second quarter were more detrimental than high proportions of the harvest taken in the first quarter. The 'best' harvest strategy, i.e. that which resulted in the highest numbers of birds and breeders after 57 years, was one that took 4%, 2%, 93% and 1% of the egg harvest in quarters one to four, respectively. Although no pairs lay their first clutch in the fourth quarter, relaying may occur during this quarter.

Sustainable egg harvests

Using the best strategy, there was no harvest rate that prevented a decrease in the mean penguin population over 57 years. At a harvest rate of 0.01 (1% of natural egg production), the adult population decreased to 96.4% of its original size after 57 years.

Oiling and rescue

Catastrophic event

When the number of birds aged two and older (adults) was reduced by one third in year ten, on average the population after a further 50 years was only 76% of what it would have been had there been no oiling (Fig. 4). After the oiling event, the population (expressed as a proportion of the no oiling scenario) increased, and then decreased again before recovering slowly on average. The initial increase resulted from birds younger than two years, which were not oiled, recruiting to the adult population. The subsequent decrease arose from reduced production of chicks in the years that immediately followed oiling.

When half of the adults oiled in year 10 were successfully rehabilitated and returned to the population at the beginning of year 11, the population on average was 88% of the 'no-oiling' level after 50 years (Fig. 4). This represented a population 12% larger than that when no rehabilitation was implemented.

Chronic, low-level oiling

The impact of chronic, low-level oiling that in each year from year 10 onwards affected 0.24% of birds aged two or older (adults), varied with the level of disturbance caused during collection of birds for rehabilitation (Fig. 5). When all oiled

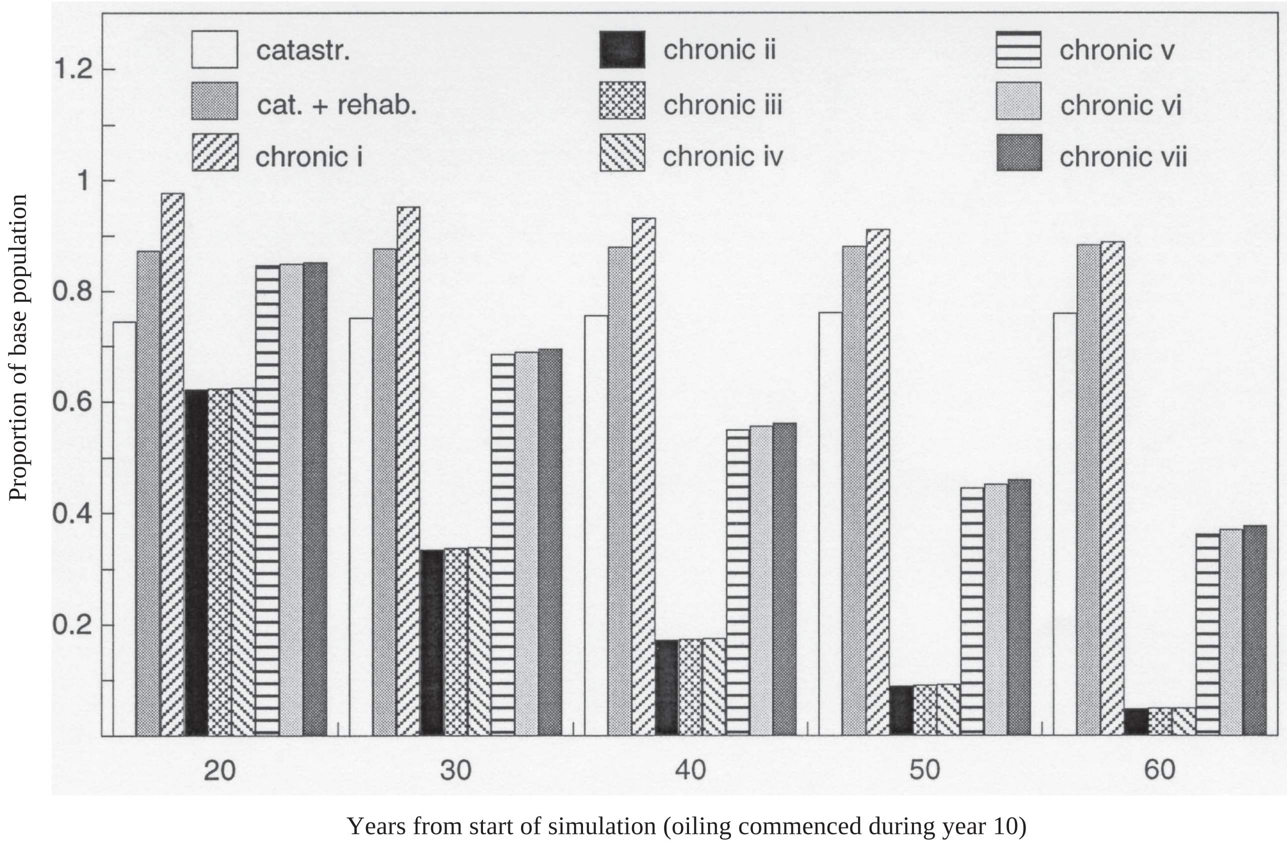

Fig. 5. *Mean numbers of African Penguins aged two years and older, when oiling events with and without rehabilitation were modelled, expressed as a proportion of the mean population which would have existed in the absence of oiling. The proportion is plotted for every 10 years after oiling, which took place in year 10, until 50 years following first oiling, for the following scenarios:*
a) a catastrophic oiling event without rehabilitation,
b) a catastrophic oiling event with rehabilitation,
c) low-level chronic oiling without searches for oiled birds or rehabilitation,
d) low-level chronic oiling when daily searches were made for oiled birds and three clutches were lost per oiled bird collected,
e) low-level chronic oiling when daily searches were made for oiled birds and two clutches were lost per oiled bird collected,
f) low-level chronic oiling when daily searches were made for oiled birds and one clutch was lost per oiled bird collected,
g) low-level chronic oiling when weekly searches were made for oiled birds and three clutches were lost per oiled bird collected,
h) low-level chronic oiling when weekly searches were made for oiled birds and two clutches were lost per oiled bird collected,
i) low-level chronic oiling when weekly searches were made for oiled birds and one clutch was lost per oiled bird collected.

birds were presumed to die (no rehabilitation), the adult population expressed as a proportion of the population which would have existed had no oiling occurred, decreased to 89% after 50 years. When oiled birds were collected for rehabilitation once a week, the adult population was between 36% and 38% of the 'no-oiling' level after 50 years. This was much higher than the 5% level resulting after 50 years of simulation when daily searches for oiled birds were modelled (Fig. 5).

When searches for oiled birds were undertaken daily, implying 80% of the oiled birds were successfully rehabilitated and 40% of the remaining clutches were lost, populations after 50 years were 4.81%, 4.90% and 4.91% of the 'no-oiling' level when three, two and one clutches respectively were lost per oiled adult collected. When searches were at weekly intervals, implying 70% of the oiled birds were successfully rehabilitated and 14% of remaining clutches were lost, populations after 50 years were 36.2%, 37.0% and 37.8% of the 'no-oiling' level when three, two and one clutches were lost per oiled bird collected. Two-way analysis of variance without replication showed that annual population sizes, when losses of one, two or three clutches per oiled bird were modelled, differed significantly from one another (*F-statistic* = 11.46, one degree of freedom, $P = 0.0013$ for weekly searches; *F-statistic* = 15.23, one degree of freedom, $P = 0.0002$ for daily searches).

Comparison of catastrophic and low-level chronic oiling

Figure 6 compares the impacts of a catastrophic oiling event at the end of year 10, and low-level chronic oiling from year 10 onwards. At the end of year 60, the mean number of adults, expressed as a proportion of the mean number alive, had no oiling occurred, was highest when there was chronic, low-level oiling without searches for oiled birds, i.e. all oiled birds were left to die. At this stage, the mean number of adults alive was only marginally greater than the mean number after a once-off catastrophic oiling event in year 10 with rehabilitation. When searches for oiled birds were made on a weekly basis in the low-level chronic situation, and one clutch was lost per oiled bird collected, the population on average decreased to match the catastrophic oiling scenario with no rehabilitation by year 26, i.e. after 16 years of low-level chronic oiling (Fig. 6). With daily searches, the same decrease was modelled after only seven years of low-level chronic oiling.

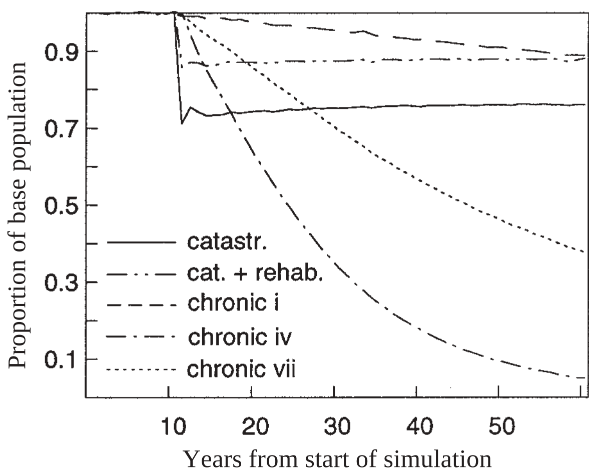

Fig. 6. *Comparison of mean numbers of African Penguins aged two years and older at Dyer Island, when chronic and catastrophic oiling events with and without rehabilitation were modelled, expressed as a proportion of the mean population which would have existed in the absence of oiling.*
The proportion is plotted every year for 50 years following commencement of oiling in year 10, for the following scenarios:
a) a catastrophic oiling event without rehabilitation,
b) a catastrophic oiling event with rehabilitation,
c) low-level chronic oiling without searches for oiled birds or rehabilitation,
d) low-level chronic oiling when daily searches were made for oiled birds and one clutch was lost per oiled bird collected,
e) low-level chronic oiling when weekly searches were made for oiled birds and one clutch was lost per oiled bird collected.

DISCUSSION

First-year survival

The mean proportion of first-year birds required to survive in order to keep an African Penguin population in equilibrium, in the absence of harvesting and oiling, was 0.51. Randall (1983) estimated first-year survival at St Croix Island to vary between 0.04 and 0.35. Other estimates of first-year survival include a minimum of 0.13 at Marcus Island (La Cock *et al.* 1987) and 0.69 at Dyer Island (La Cock & Hänel 1987). The modelled mean falls between these values.

Egg harvests at Dassen Island

The simulated proportion of all eggs laid that was harvested, which best fitted the actual decrease in eggs collected, was 0.48. This indicates that the level of harvesting was exceptionally high. A two-foot (0.6 m) wall was built around Dassen Island to exclude penguins from the interior of the island, and thereby facilitate egg collecting (Rand 1963). The date of erection of this wall is uncertain. Walls for the protection of seabirds at guano islands were constructed from about 1937 onwards (Hewitt 1937). The penguin exclusion walls at Dassen Island were built between this date and early 1942 (Price 1942). The wall may have increased the proportion of eggs harvested.

It is worth noting that present-day parameters used in this modelling study may differ from those earlier this century, when the food supply for African Penguins was more robust. Crawford (1998) suggests that increased competition for food over the last six decades may have resulted in reduced chick production or reduced survival of juvenile African Penguins. In this event, the measured decrease in eggs harvested at Dassen Island during the first half of the 20th Century would have necessitated removal of an even greater proportion (more than 50%) of all eggs laid.

Population size at Dassen Island

Nicoll (1906, 1908) was told by a lighthouse keeper in February 1906 that there were nine million penguins at Dassen Island. Kearton (1930) wrote that there were at least five million penguins at Dassen Island. Westphal & Rowan (1971) estimated there were 1.5 million penguins at Dassen Island between 1900 and 1930. For the same period, from collections of eggs, Frost *et al.* (1976) calculated the breeding population to be at least 300 000 birds. Model estimates of the population in 1910 were 1.45 million adults and 0.57 million breeding pairs, i.e. 1.14 million breeding adults. These results best match the estimate of Westphal & Rowan (1971).

In a recent assessment of the decrease of the African Penguin population through the 20th Century, Crawford *et al.* (1995) adopted the estimate of Frost *et al.* (1976) to suggest a decrease of 90% of the penguin population at Dassen Island. In the early 1990s, there were about 30 000 African Penguins in adult plumage at Dassen Island (Crawford *et al.* 1995). If model results for the number of penguins at Dassen Island in 1910 are accepted, the actual decrease this century is 98%.

On aerial photographs of Dassen Island taken in November 1956, 80 562 penguins were counted (Rand 1963). There was incomplete coverage of the island and an unknown number of penguins were absent from the island. This led Rand (1963) to estimate that the number of penguins at Dassen Island was 145 000 birds. The mean number of adults estimated by the model for 1956 was 216 000, but with a high standard deviation. Rand's (1963) estimate may or may not have been a good one. We were unable to generate a precise estimate from the model. However, the model tracked the decreasing egg harvest reasonably well (Fig. 2), suggesting that its mean estimates of population size are realistic. The modelled harvest of eggs in 1915 was higher than recorded, but the actual harvest was 10–30% higher than the recorded harvest, because many eggs were discarded after testing (Siegfried & Crawford 1978). By using recorded egg harvests and the modelled exploitation rates, a conservative estimate of egg production in 1910 was generated. This avoided possible overestimation of the population size from overestimating the under-reporting of egg harvests. The rate of decrease in egg harvests would not have been affected by under-reporting, provided the proportion of discarded eggs was constant throughout the collection period.

Season of egg harvests

There was not a great difference for the penguin population when harvesting of eggs was undertaken in different seasons. The strategy that had least impact on the population was for most eggs to be collected in the third quarter, when only 4% of birds lay their first clutches, but when relaying also occurs. It was not possible to take a substantial harvest in the fourth quarter, because few eggs are produced then.

If there is a lower survival of eggs and chicks in the latter part of the breeding season, the harvesting of eggs in the second half of the year may have a smaller impact. There is no clear evidence of different survival rates through the year, but we have observed abandonment of chicks by parents going into moult towards the end of the year. Success of clutches laid in different seasons needs further investigation. Although egg harvests are unlikely to be resumed in the foreseeable future, the results are also applicable to factors having a similar influence to egg harvests. These include, for example, losses of clutches as a result of human disturbance, such as during collection of oiled birds.

Sustainability of egg harvests

Even the smallest egg harvests caused the population to decline. Incorporation of density dependence in the model may alter this outcome.

Oiling and rescue

Kruger (1949) thought that it would take African Penguins at Dyer Island at least half a century to recover following the loss of one third of the population to oiling. This appears to have been an optimistic assessment. On average, after 50 years the population would have been at only 76% of its level in the absence of oiling had there been no rehabilitation. Assuming half the birds were successfully rehabilitated, this level would have been 88%. These should be viewed as preliminary results because density-dependence effects on survival have not as yet been incorporated into the model. Modelling density-dependence will be the next step towards improved assessment of the impacts of oiling and disturbance on African Penguins.

In the long term, the impact of low-level chronic oiling without searches for contaminated birds matched the effect of a catastrophic oiling event when birds were rehabilitated. When searches were made for oiled birds, the average population was estimated to decrease rapidly to very low levels, well below those caused by a catastrophic spill in which no rehabilitation was undertaken (Fig. 6).

This result is dependant on the degree of disturbance assumed to result from searching for and collecting oiled birds, with losses during searches especially important (Fig. 5). The disturbance effects noted by Hockey & Hallinan (1981) were used. The applicability of these needs fuller investigation. For example, it may be that birds become accustomed to human presence. Further field tests are necessary. There will certainly be inter-island differences in the amount of losses caused by disturbance. At islands where most penguins nest in burrows, such as Dassen Island, losses will be less than in surface-nesting situations, e.g. Dyer Island.

If disturbance persists at the high level reported by Hockey & Hallinan (1981), from a population perspective it would be better not to search for oiled birds. If any searches are made, these should be at a low frequency, e.g. weekly searches have much less impact than daily searches. Management should aim to develop methods for identifying and collecting oiled birds that will minimise losses of clutches from disturbance, e.g. catching oiled birds at landing places away from the breeding colonies.

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