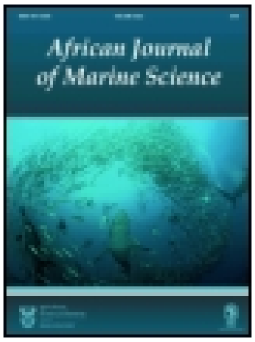

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Restoration of oiled African penguins *Spheniscus demersus* a decade after the *Apollo Sea* spill

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The bulk ore carrier *Apollo Sea* sank south-west of Dassen Island off western South Africa in June 1994, oiling approximately 10 000 African penguins *Spheniscus demersus*, most of which were collected from Dassen Island. A total of 4 076 de-oiled penguins was released with flipper bands. From 1994 to 2005, follow-up research using re-sighting and capture-mark-recapture methods indicated that about 73% of the de-oiled penguins observed back at Dassen Island attempted to breed, and were thus successfully restored into the breeding population. For de-oiled breeders, the median interval between their first recorded sighting and first recorded breeding attempt was 11 months, indicating a short-term delay in restoration. At least 45% of the de-oiled breeders were still being re-sighted five years after their release, and a minimum of 4% survived into their ninth year. These results represent the most successful restoration estimates anywhere in the world. The proportion of de-oiled juvenile penguins re-sighted back at Dassen Island and recorded breeding was lower than that of birds in adult plumage. De-oiled non-breeders spent significantly more time along the shore and less time within breeding colonies than de-oiled breeders. The mean proportion of de-oiled breeders that abstained from breeding each year during the study period was greater than expected. There was a negative relationship between breeding and subsequent survival and breeding, suggesting a cost of reproduction for de-oiled birds.

Keywords: African penguin, *Apollo Sea*, breeding, capture-mark-recapture, Dassen Island, de-oiling, oiling, rehabilitation, restoration, South Africa, *Spheniscus demersus*

Introduction

The coastal waters of South Africa, and especially the south-western coasts, are a global hotspot for oil pollution (Moldan and Dehrmann 1989, Nel and Whittington 2003). The African penguin *Spheniscus demersus*, classified as Vulnerable because of its continued population decline (Crawford 2000, Whittington *et al.* 2000, du Toit *et al.* 2003, IUCN 2007), is one of the species most threatened by oil pollution in southern Africa. The rate of oiling has increased markedly over the past few decades (Adams 1994, Whittington 2002, Wolfaardt *et al.* in press d); 77% of all penguins oiled between 1968 and 2002 were recorded between 1991 and 2000 (Nel *et al.* 2003), mostly as a result of two large oil spills, the *Apollo Sea* in June 1994 (Underhill *et al.* 1999) and the *Treasure* in 2000 (Crawford *et al.* 2000). Oil pollution is considered to be one of the main threats to the African penguin (Whittington *et al.* 2000, Nel *et al.* 2003).

The closure of the Suez Canal in 1967 and the diversion of oil tankers around southern Africa resulted in increased contamination of seabirds, especially African penguins (Westphal and Rowan 1969). A large oil spill near Cape Town in 1968 led to the establishment of the Southern African Foundation for the Conservation of Coastal Birds (SANCCOB), whose primary aim is to clean and rehabilitate oiled seabirds (Westphal and Rowan 1969, Morant *et al.* 1981, Moldan and Westphal 1989, 1994). The biological and conservation value of rehabilitation as a wildlife management intervention has been questioned (Estes 1991, Boersma 1995, Anderson *et al.* 1996, Sharp 1996), including the conservation for African penguins (Frost *et al.* 1976). The design of a stainless steel flipper band for the African penguin (Jarvis 1970, Cooper and Morant 1981) has made it possible to test the effectiveness of cleaning efforts. Subsequent post-release studies have shown that, in contrast to rehabilitation of seabirds elsewhere (e.g. Khan and Ryan 1991, Sharp 1996, Wernham *et al.* 1997), de-oiled African penguins have a high survival rate (Randall *et al.* 1980, Morant *et al.* 1981), similar to that of non-oiled birds (Underhill *et al.* 1999, Whittington 1999a, 2002). Evidence from these studies suggests that rehabilitation of oiled African penguins makes an important contribution to the conservation of this species. Further, the cost of de-oiling African penguins in large oil spill events is substantially lower than in other parts of the world, ranging between US$90 and US$112 per penguin rescued, de-oiled and released back into the wild (Nel *et al*. 2003, Wolfaardt *et al.* in press d).

However, in conservation terms, rehabilitation of birds is of little value unless they breed again. The overall success of the rehabilitation process should also take into account the reproductive output of birds after release. If rehabilitated birds survive for months or years, but never produce offspring, they are effectively redundant to the population. It can even be argued that rehabilitated birds that never produce offspring actually have a potentially negative impact on the breeding population by competing for scarce resources. In this study, a rehabilitated bird is one that has been de-oiled (cleaned, treated and subsequently released), and has survived in the wild for at least one month. The term 'restored' is used for rehabilitated birds that have been found breeding in the wild (Underhill *et al.* 1999).

Randall *et al*. (1980) followed the fate of 150 African penguins oiled at St Croix Island, South Africa, over a period of six months. Of the 106 birds that were released, 80 were re-sighted at the island, and six were recorded breeding. Morant *et al*. (1981) reported that 20% of the rehabilitated birds seen back at colonies after seven major oiling incidents, including the St Croix spill, had been recorded breeding. Unfortunately, those authors did not indicate the degree of search effort or the period over which re-sightings were attempted. The main objective of these early studies was to establish that some de-oiled penguins did breed, but they were not sufficiently intensive to estimate whether all de-oiled penguins breed again, or if there was a proportion that does not breed. Giese *et al*. (2000) and Goldsworthy *et al.* (2000) studied the post-release survival and breeding success of rehabilitated oiled little penguins *Eudyptula minor* over a two-year period, but did not report the proportion of oiled rehabilitated birds attempting to breed.

The bulk ore carrier *Apollo Sea* sank south-west of Dassen Island (33°25′ S, 18°05′ E) at approximately 33°32′ S, 17°50′ E in June 1994 (Erasmus 1995). Heavy fuel oil washed ashore at both Dassen and Robben (33°48′ S, 18°23′ E) islands, contaminating about 10 000 penguins (Dehrmann 1994a). About 7 200 of these were caught at Dassen Island and 2 400 at Robben Island; the remainder were caught at other island colonies and on the mainland coastline (Crawford 1994, 1995, Dehrmann 1994a). For details of how contaminated penguins are de-oiled and treated at SANCCOB, see Barrett *et al.* (1995) and Parsons and Underhill (2005). Approximately 4 800 (48%) of the oiled penguins were successfully released after de-oiling; of the 52% that died, about half of the deaths occurred in the first 48 hours after collection (Williams 1995a).

In this paper, we document the systematic follow-up of de-oiled African penguins after the *Apollo Sea* oil spill over a period of 10.5 years, from September 1994 up until March 2005, to assess the restoration success of cleaning oiled African penguins. Previous studies focused mostly on the post-release survival, and rehabilitation success, of the oil spill victims over a 3–5 year period (Underhill *et al.* 1997, 1999, 2000, Whittington 2002). The aim of this study is to examine the extent to which de-oiled African penguins are successfully restored into the breeding population, thereby allowing a better assessment of the conservation value of cleaning oiled birds for this species.

Material and Methods

Study area

Dassen Island is located approximately 55 km north-west of Cape Town (Figure 1). It is an 'Important Bird Area' (Barnes 1998), and supported the world's largest African penguin colony during the period of the study (du Toit *et al.* 2004). Over 90% of the penguins breed under cover in burrows, in among granite boulders or under shrubs; the remainder nest in the open (ACW unpublished data). The island is divided into nine monitoring areas and management areas, Areas A–I (Figure 2).

A total of 4 076 de-oiled penguins was released with flipper bands, most at Silwerstroomstrand (33°34′ S, 18°21′ E), a mainland beach between Dassen and Robben islands (Underhill *et al.* 1999). This total comprised 3 488 birds in adult plumage and 348 in juvenile plumage, hereafter referred to as *Apollo Sea* adults and juveniles respectively. An additional 240 flipper-banded birds that were released did not have their age recorded on the banding schedules. The re-sighting analyses of all *Apollo Sea* birds conducted by Whittington (2002) indicate that the majority of these birds were likely to have been adults and were treated as such in this study. All birds were released between 26 July and 11 September 1994 (Underhill *et al.* 1999). It is not known what proportion of the birds that survived the cleaning process and were ultimately released originally came from Dassen and Robben islands. Unfortunately, about 700 de-oiled birds were released without flipper bands, and these were therefore indistinguishable from birds that were never oiled.

Systematic searches were conducted for flipper-banded penguins at Dassen Island from September 1994, one month after most of the penguins had been released; in this paper we report results until March 2005. Each flipper band has a unique number and can be read from a distance of up to 50 m with a spotting scope. We used binoculars and a spotting scope to search for flipper-banded penguins along the shore during weekly coastal surveys. Re-sighting effort during coastal surveys was greater in the period 1994–2000 than from 2001 to 2005. We examined all nest sites and recorded flipper-bands during surveys of two breeding study colonies set up as part of this study, Area G and Area B (Figure 2). These were the colonies on Dassen Island where the largest numbers of oiled penguins had been caught (AJ Williams, Western Cape Nature Conservation Board, pers. comm.), and hence where the most intensive monitoring took place. Until the end of 1995, surveys were monthly; thereafter they took place twice a month. We also conducted surveys of all nest sites in two smaller study areas (within Areas F and D), monthly until the end of 1995 and twice monthly thereafter. An additional study area was set up in Area A in May 1997, which was surveyed fortnightly until the end of the study period. During

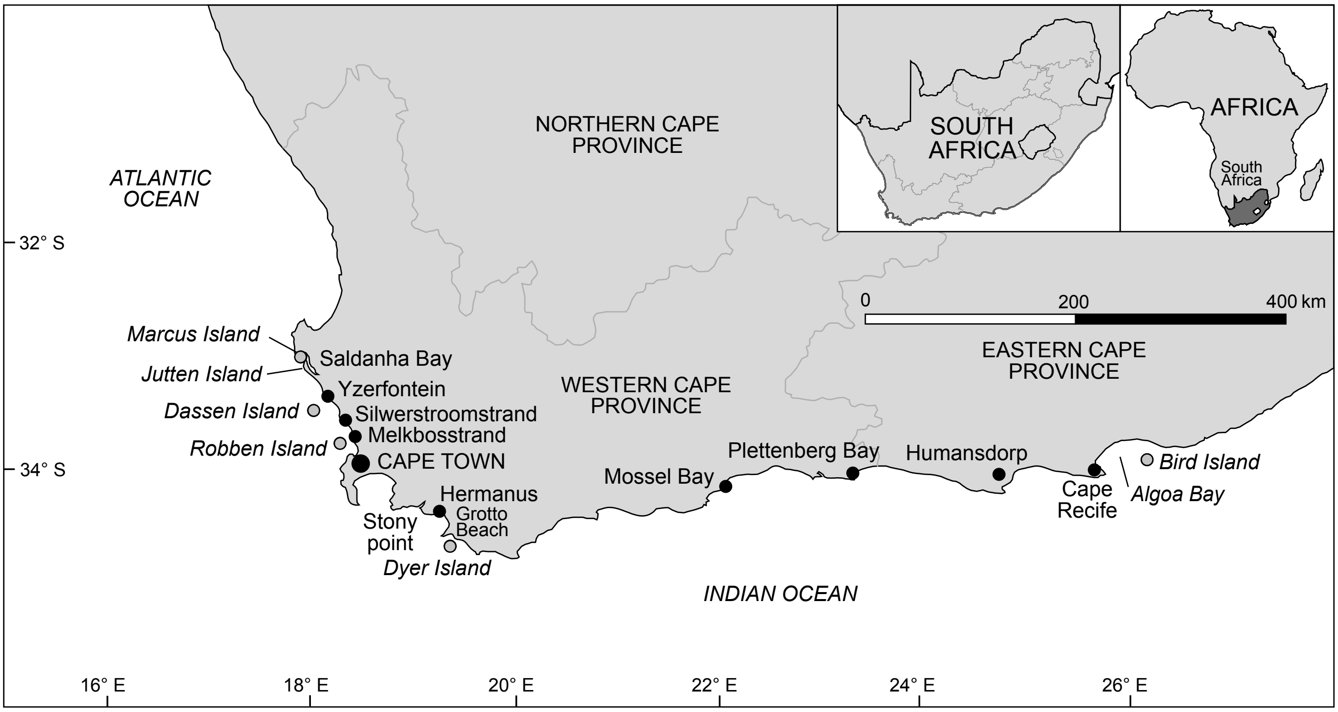

Figure 1: Location of Dassen Island, and other penguin colonies and localities mentioned in the text

the annual island-wide breeding censuses, all nests were searched for flipper-banded penguins. In addition, we opportunistically recorded re-sightings of flipper-banded birds during the course of the study period. The activity of the bird for each re-sighting was noted and placed into one of the following broad categories: moulting, breeding (which was further divided into the numbers of eggs and chicks), pairs and loafing (a single bird not engaged in any of the other activities). A bird was regarded as breeding only if it was observed incubating eggs or brooding or guarding chicks. Birds observed together as pairs but without eggs or chicks were not recorded as breeders. For each re-sighting, we also recorded the management area (A–I), the locality (whether the bird was observed on the beach or in a breeding colony), as well as the nest type (where relevant). All re-sighting data were incorporated into a database for further analysis. We also checked data from the South African Bird Ringing Unit (SAFRING) relating to African penguins flipper-banded, re-sighted and recovered dead at other localities, because some birds are known to move between different colonies (Whittington *et al.* 2005c). We investigated the number of oil spill survivors and the proportion of those released that were recorded breeding for two age classes of birds: birds released in adult plumage (n = 3 728) and those released as juveniles (n = 348).

We compared whether there was a tendency for de-oiled birds that were never recorded breeding to be seen less frequently in a breeding colony as opposed to on a landing beach. For each bird, the number of re-sightings in the colony and the number of re-sightings on the beach were recorded. These were used as explanatory variables in a logistic regression with the response variable being whether the bird had been recorded breeding (response = 1) or not (response = 0). Due to the low number of un-oiled penguins that were flipper-banded, and a temporary moratorium on flipper-banding at the time the study was initiated, we were unable to include an un-oiled control group in this analysis.

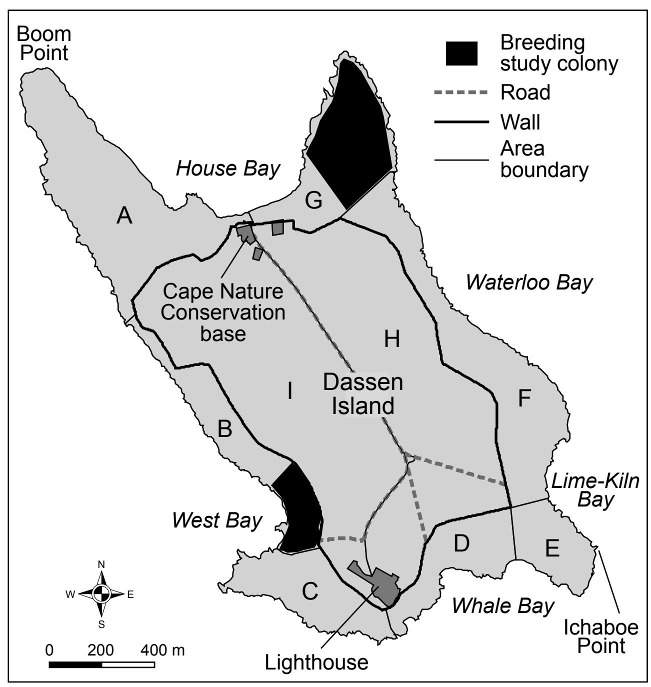

Figure 2: Locations of management and monitoring areas (Areas A–I) at Dassen Island, and the African penguin breeding study colonies in Areas B and G

Capture-mark-recapture analyses

Multistate capture-mark-recapture (CMR) models were used to estimate the probability of adult penguins attempting to breed after having been de-oiled, and to estimate the survival of birds in each state. In the model, penguins assumed one of three different reproductive states each year: non-breeder (n), breeder (b) and secondary non-breeder (s) (Figure 3); breeders were birds that were observed incubating eggs, brooding or guarding chicks (i.e. breeding) during the current year; and secondary non-breeders did not reproduce during the current year, but had been recorded breeding previously (post de-oiling). We are confident that all breeding birds were observed, and the risk of misclassifying an individual in any given year was thus small. The reason for including a secondary non-breeder state was to examine possible costs of breeding for birds that were de-oiled. Furthermore, these birds were suspected to have different recapture probabilities to those in other states. CMR models allow a distinction to be made between survival and the recapture probability (the probability of being recaptured at a certain occasion given that the individual was alive) (Lebreton *et al.* 1992, Nichols *et al.* 1994). The design is based on the approach outlined in McElligott *et al.* (2002).

A capture history matrix was constructed for each adult *Apollo Sea* survivor that was seen back at Dassen Island, and also included observations of these birds at other colonies. Recapture periods were not calendar years, but were set to start in March and end in February of the following year, except for 1994, which started in September 1994 (the beginning of the study) and ended in February 1995. The February–March recapture period was set to coincide with the end of the peak moult period (February) for penguins at Dassen Island (Wolfaardt *et al.* in press c).

We first examined the survival and breeding of all adult de-oiled birds subsequently observed on Dassen Island. For this analysis, we used the first sighting of the individual, at Dassen Island, either as a non-breeder or a breeder, as the initial sighting. It is likely, however, that the data contained transients (birds that came ashore at colonies other than their own, moving on to their resident colonies thereafter), especially among non-breeders. Because it was not possible to distinguish between permanent emigration and mortality, transients would have resulted in survival being underestimated during the interval after the initial sighting. This transient effect was accounted for by allowing survival to be lower during those intervals (Pradel *et al.* 1997). Banded penguins were re-sighted in all areas of the island, but most intensively in Area G and Area B. The CMR analysis was restricted to these two study areas. Preliminary analyses showed no evidence for differences between the areas in any of the parameters, and the data were thus pooled. The capture history of the de-oiled birds re-sighted at Dassen Island also included observations of these birds at other colonies, which were obtained from the SAFRING database.

The most general model included a transients effect, independent time effects on survival and recapture in all three stages, and time dependence in the three possible transition rates (Model 12, Table 1). The goodness-of-fit for this model was assessed using the median-$\hat{c}$ approach in the program MARK (White and Burnham 1999). With five replicate simulations at 10 levels of overdispersion, this test showed that the overdispersion in the data was small ($\hat{c}$ = 1.087), and that the model was therefore a good starting point for model selection. All other models were simplified versions of this general model. The relative performance of all models were assessed using Akaike's Information Criterion, adjusted for sample size (AICc); the best model is the one with the lowest AICc value (Burnham and Anderson 2002). All models were fitted using program MARK 4.3 (White and Burnham 1999). Parameter estimates and confidence intervals are reported from Model 2, which differed only marginally from Model 1 in its AICc, and was more parsimonious (Table 1).

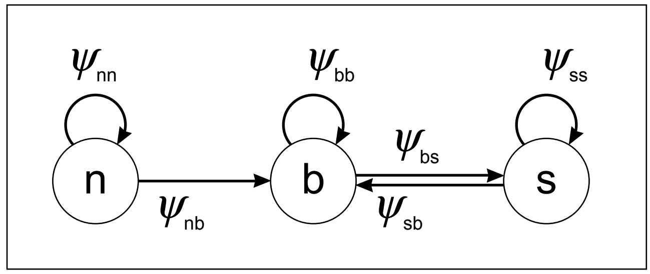

Figure 3: Diagram showing the states used in the multistate capture-mark-recapture analyses for African penguins on Dassen Island. Penguins can either be non-breeders (n), breeders (b), or secondary non-breeders (s). Recapture and survival rates were estimated separately for each state, and the probabilities of moving between states (ψ) were also estimated. The way in which the states were defined results in non-breeders being unable to become secondary non-breeders directly, but breeders cannot move back to the initial non-breeder stage. These transition rates were thus fixed to zero in the analyses. See text for further details

The main objective of the CMR analyses was to determine whether there were differences in survival between birds in each stage, and the probability of changing between different states. The above analyses provided these estimates for birds that arrived back at Dassen Island. However, an additional objective of the study was to determine how long it took for de-oiled penguins to start breeding after they had been released from the rehabilitation centre. Therefore, we used banding at the rehabilitation centre (SANCCOB) as the first observation for each individual, at which point all birds were classified as non-breeders. For this analysis, we included only individuals that were later encountered at Dassen Island; it does not therefore provide estimates of breeding probabilities for all de-oiled penguins. Rather, we examined the surviving part of the Dassen Island population to determine when they started breeding again after having been de-oiled.

Results

Re-sightings

Between September 1994 and March 2005, we re-sighted a total of 2 499 *Apollo Sea* survivors at Dassen Island. Of these individuals, 2 444 were birds that were released in adult plumage (65% of those released in adult plumage) and 55 were birds released in juvenile plumage (16% of those

Table 1: Summary of model selection of multistate capture-mark-recapture analysis for de-oiled African penguins at Dassen Island, 1994–2005. The models consisted of nine parts: three parts modelling survival in each breeding state (S_n, S_b, S_s for non-breeder, breeder and secondary non-breeder respectively); three parts modelling the recapture rates in these states (P_n, P_b, P_s); and three parts modelling transitions between states (ψ_{nb}, ψ_{bs}, ψ_{sb}, see Figure 3). All components were modelled as variable over time (t) or constant (.). Equality of survival or recapture in different states is indicated by = between the relevant model parts, and // denotes models which enforced parallel time variation in two model components. All models except Model 17 include transients effects. The models were assessed by Akaike's Information Criterion (AICc), and the difference between each model and the best one is given (ΔAICc). The relative performance of each model compared with the other ones in the set is measured by the Akaike weight, and this weight is used in the model averaging process. *K* is the number of parameters

	Model	AICc	ΔAICc	Akaike weight	*K*	Deviance
1	$S_n(t)=S_b(t)//S_s(t)P_n(t)P_b(.)P_s(t)\psi_{nb}(t)\ \psi_{bs}(t)\ \psi_{sb}(t)$	16 852.363	0.000	0.454	69	4 666.026
2	$S_n(t)=S_b(t)//S_s(t)P_n(t)//P_s(t)P_b(.)\psi_{nb}(t)\ \psi_{bs}(t)\ \psi_{sb}(t)$	16 852.430	0.067	0.439	60	4 684.454
3	$S_n(t)=S_b(t)S_s(t)P_n(t)//P_s(t)P_b(.)\psi_{nb}(t)\ \psi_{bs}(t)\ \psi_{sb}(t)$	16 855.838	3.475	0.080	69	4 669.501
4	$S_n(t)=S_b(t)S_s(t)P_n(t)P_b(.)P_s(t)\psi_{nb}(t)\ \psi_{bs}(t)\ \psi_{sb}(t)$	16 858.151	5.788	0.025	78	4 653.402
5	$S_n(.)S_b(t)//S_s(t)P_n(t)P_b(.)P_s(t)\psi_{nb}(t)\ \psi_{bs}(t)\ \psi_{sb}(t)$	16 863.296	10.933	0.002	79	4 656.498
6	$S_n(t)S_b(t)S_s(t)P_n(t)P_b(.)P_s(t)\psi_{nb}(t)\ \psi_{bs}(t)\ \psi_{sb}(t)$	16 868.503	16.140	0.000	86	4 647.345
7	$S_n(t)=S_b(t)S_s(t)P_n(t)P_b(.)P_s(t)\psi_{nb}(t)\ \psi_{bs}(t)//\psi_{sb}(t)$	16 875.145	22.782	0.000	69	4 688.809
8	$S_n(t)=S_b(t)=S_s(t)P_n(t)P_b(.)P_s(t)\psi_{nb}(t)\ \psi_{bs}(t)\ \psi_{sb}(t)$	16 878.365	26.002	0.000	69	4 692.029
9	$S_n(t)S_b(t)S_s(.)P_n(t)P_b(.)P_s(t)\psi_{nb}(t)\ \psi_{bs}(t)\ \psi_{sb}(t)$	16 881.210	28.847	0.000	79	4 674.412
10	$S_n(t)S_b(t)=S_s(t)P_n(t)P_b(.)P_s(t)\psi_{nb}(t)\ \psi_{bs}(t)\ \psi_{sb}(t)$	16 882.619	30.256	0.000	78	4 677.870
11	$S_n(t)=\ S_s(t)S_b(t)P_n(t)P_b(.)P_s(t)\psi_{nb}(t)\ \psi_{bs}(t)\ \psi_{sb}(t)$	16 882.727	30.364	0.000	78	4 677.978
12	$S_n(t)S_b(t)S_s(t)P_n(t)P_b(t)P_s(t)\psi_{nb}(t)\ \psi_{bs}(t)\ \psi_{sb}(t)$	16 884.953	32.590	0.000	94	4 647.345
13	$S_n(t)S_b(t)S_s(t)P_n(t)P_b(.)P_s(t)\psi_{nb}(t)\ \psi_{bs}(t)\ \psi_{sb}(.)$	16 887.157	34.794	0.000	79	4 680.360
14	$S_n(t)S_b(.)S_s(t)P_n(t)P_b(.)P_s(t)\psi_{nb}(t)\ \psi_{bs}(t)\ \psi_{sb}(t)$	16 890.449	38.086	0.000	78	4 685.700
15	$S_n(t)S_b(t)S_s(t)P_n(t)P_b(.)P_s(t)\psi_{nb}(t)\ \psi_{bs}(.)\ \psi_{sb}(t)$	16 892.493	40.130	0.000	78	4 687.744
16	$S_n(t)S_b(t)S_s(t)P_b(.)P_n(t)=P_s(t)\psi_{nb}(t)\ \psi_{bs}(t)\ \psi_{sb}(t)$	16 897.744	45.381	0.000	77	4 695.043
17	As Model 6, but no transients effect	16 918.851	66.488	0.000	77	4 716.150

released in juvenile plumage). These juvenile penguins re-sighted did not represent the total number of de-oiled juveniles re-sighted, only those observed at Dassen Island; an additional 50 juveniles had been re-sighted at other colonies by 1999 (Whittington 2002). Nine penguins were found dead during their first post-release moult as a result of gangrene poisoning caused by the flipper bands having been fitted too tightly (Underhill 1995). The tight bands did not allow sufficient space for the expansion of the flipper during moult, causing wounds to develop that subsequently became gangrenous. Consequently, we conducted searches for other penguins with flipper bands that had been fitted too tightly. As a precaution, 69 ill-fitted flipper bands were removed from penguins on Dassen Island, which were then released without bands. These birds were excluded from all further analyses. The numbers and proportions of *Apollo Sea* survivors reported here represent only those birds sighted at Dassen Island, and do not reflect the total number sighted after release. Re-sighting information for birds that were observed at Dassen Island and also at other colonies is included. Some 10% (n = 240) of the adult *Apollo Sea* birds re-sighted at Dassen Island were also observed at other colonies. Re-sightings of these birds at colonies other than Dassen Island amounted to an additional 577 observations.

Birds recorded breeding

By March 2005, 1 459 (61%) of the de-oiled adult birds that had been re-sighted at Dassen Island had been recorded breeding (Figure 4); the proportion increased to 70% and 74% when the analysis was restricted to birds observed in Areas G and B respectively (Table 2). The majority of these birds (97%) were recorded breeding at Dassen Island. Of 45 birds observed at least once at Dassen Island and recorded breeding elsewhere, 43 were recorded breeding at Robben Island, and two at Jutten Island (33°05′ S, 17°58′ E) (Figure 1). The number of de-oiled birds that were recorded breeding at Dassen Island, and which were also observed (but not breeding) at other colonies, was 106; Robben Island was the colony visited on the majority (85%) of these occasions. The pattern of cumulative re-sightings of de-oiled birds over time was similar for the island as a whole and for Areas G and B, in terms of both the birds re-sighted and those recorded breeding. In all three cases, the cumulative figures became almost stable by the end of 1997, approximately 30 months after the birds were released. However, we continued to re-sight and record breeding small numbers of previously unrecorded birds up until June 2004. In all, 22 of the re-sighted juveniles (40% of those re-sighted at Dassen Island) had been recorded breeding by March 2005. All but two of these birds bred at Dassen Island. The other breeding attempts were at Robben and Jutten islands.

Of the adult birds recorded breeding during the study, over 70% were first re-sighted as breeders by the end of 1996, within 28 months of their release (Figure 5). The time that elapsed between release and when the birds were first recorded breeding ranged from less than a month to 115 months. The median time elapsed between release and first recorded breeding was 15 months. The median interval between when the bird was first observed at Dassen Island and when it was first recorded breeding (excluding birds that were observed breeding on the first occasion they were re-sighted) was 11.3 months (minimum, lower quartile, median, upper quartile and maximum were 0.07, 4.2, 11.3, 24.9 and 108 respectively). At least 655 of the penguins recorded as breeders (27% of those re-sighted at Dassen and 45% of those recorded breeding) were known to have survived into their fifth year following release from SANCCOB; 64 *Apollo Sea* breeders survived into their ninth year (Figure 4). The number of years in which *Apollo Sea* breeders were recorded breeding ranged from one to 10. Of these, 36 (2.5% of the total number of de-oiled *Apollo Sea* adults that were recorded breeding) were observed breeding in more than eight of the 10 years of the study.

The proportion of re-sighted birds that were recorded breeding each year increased steadily from 36% in 1994 (i.e. 36% of the birds observed in 1994 were recorded breeding in that year) to 67% in 2002 (Table 3). When the analysis was restricted to Areas G and B, the proportion breeding ranged from 37% in 1994 to 71% in 2002. The number of de-oiled birds recorded breeding peaked in 1996 (Table 3).

Non-breeders

Some 39% of the adult *Apollo Sea* survivors that were re-sighted at Dassen Island were never recorded breeding, neither at Dassen Island nor any other colony, during the time between their release in 1994 and March 2005 (Table 2). When considering only the birds observed in Areas G and B, this proportion dropped to 30% and 26% respectively (Table 2). We observed 31% of the non-breeders on only one occasion at Dassen Island (Figure 6), compared with 7% of the adult *Apollo Sea* breeders. The maximum number of times a non-breeder was observed during the study period was 33 times; this penguin was observed in every year from 1995 to 2001, and on 15 separate occasions in 1996. Non-breeders were observed in each year, from 1994 to 2005. The number of non-breeders re-sighted was at a peak in 1995 and 1996, and declined to two birds in 2005. Some 9% of the *Apollo Sea* non-breeders were also observed at other colonies, mostly (84%) at Robben Island.

In all, 77% of all observations relating to non-breeders were of birds on landing beaches, as opposed to in breeding colonies. For 2 246 de-oiled penguins for which data were available (excluding birds also observed at other colonies), we included the number of times a penguin was re-sighted on a beach (B) and the number of times it was re-sighted in a breeding colony (C) in the following generalised linear model (logistic regression) to determine the probability (p) of being a non-breeder:

$$\text{logit}(p) = 1.765 + 0.0421B - 1.5404C$$

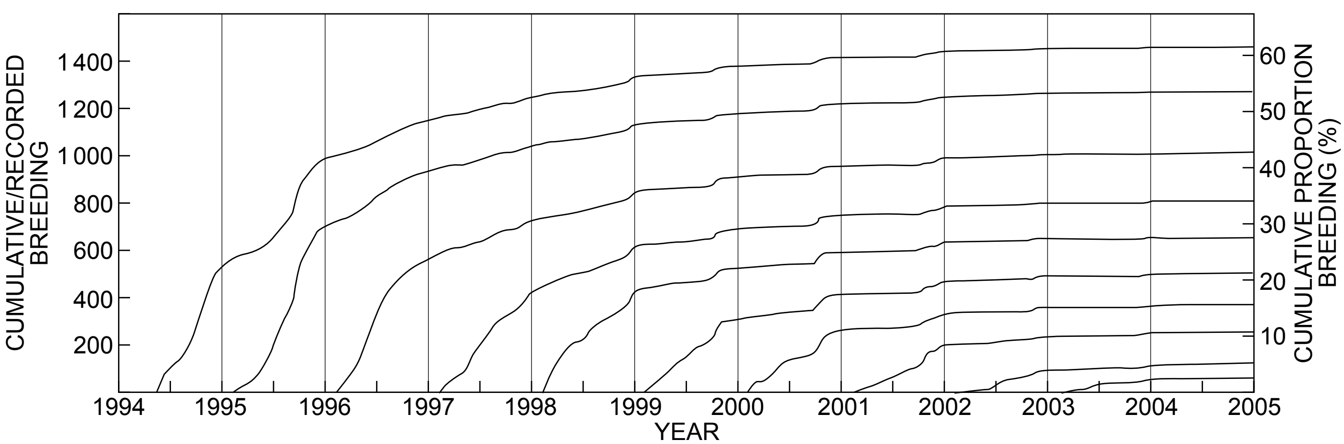

Figure 4: Cumulative totals of de-oiled adult African penguins recorded breeding following the *Apollo Sea* oil spill at Dassen Island. The first line shows the overall cumulative total from the time of release (31 July 1994) until March 2005. Each line thereafter represents the number of birds recorded breeding that survived progressive periods, from at least one year after release (in the case of the line starting at 31 July 1995) up until nine years after release (for the line labelled starting at 31 July 2003). The vertical lines represent the mid-point (1 July) of each year. The proportion recorded breeding, as a percentage of the final number of adult *Apollo Sea* survivors observed at Dassen Island during the study, is shown on the right

Table 2: Numbers of rehabilitated adult *Apollo Sea* African penguins observed and recorded breeding at Dassen Island, September 1994–March 2005

Parameter	Whole island		Area G		Area B	
	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles
Number observed	2 375[a]	55	975	19	699	13
Number recorded breeding at Dassen	1 414	20	659	9	513	6
Number recorded breeding at other colonies	45	2	19	0	2	1
Total recorded breeding	1 459	22	678	9	515	7
Number not recorded breeding	916	33	297	10	184	6
Number non-breeders observed at other colonies, but not breeding	84	12	27	4	17	4

[a] Excludes 69 birds whose bands were removed due to damage to flippers (see text)

The standard errors of the three coefficients were 0.011 ($z = 16.0$, $p < 0.001$), 0.0178 ($z = 2.37$, $p = 0.018$) and 0.0793 ($z = -19.4$, $p < 0.001$). The positive coefficient of B indicated that the more frequently the penguin was seen on the beach the more likely it was to be a non-breeder, and the negative coefficient of C indicated that the more frequently the penguin was seen in the colony the less likely it was to be a non-breeder. This model accounted for 49% of the deviance.

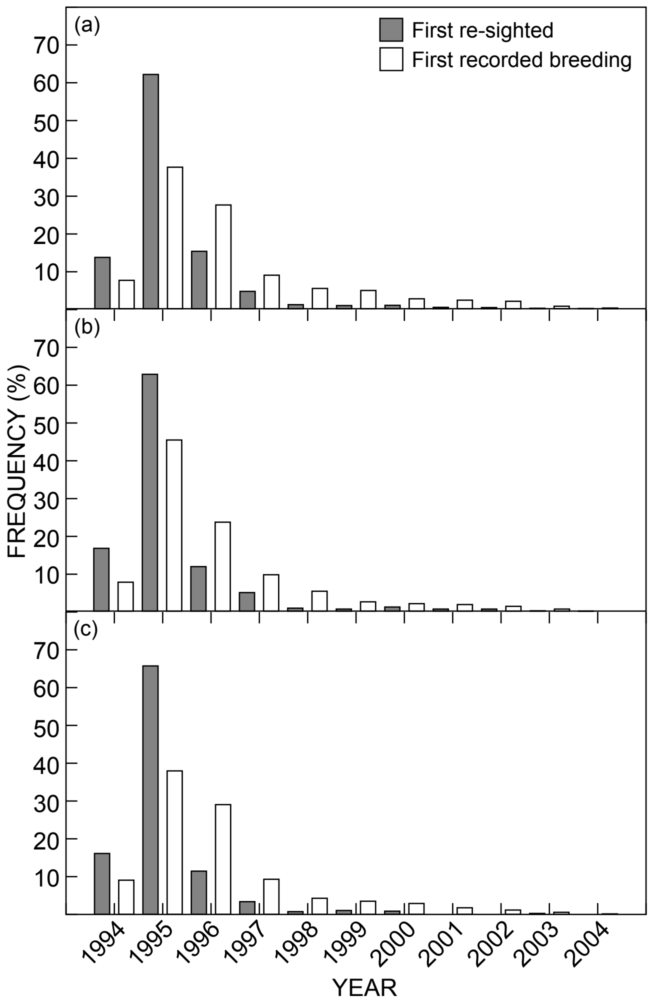

Figure 5: Percentage of de-oiled African penguins from the *Apollo Sea* spill re-sighted and recorded breeding at Dassen Island for the first time after release for (a) the whole island, (b) Area G and (c) Area B. 1994 only includes the period September–December

Of the non-breeders that were observed in a breeding colony, 268 (29% of the total number of non-breeders re-sighted during the study) were recorded on a nest site (Table 4). This increased to 35% and 41% when the analysis was restricted to Areas G and B respectively (Table 4). Of the activities recorded for each re-sighting, the 'pair' activity is the closest to a breeding activity. This activity describes a pair of birds actively defending a nest site, and normally forms part of the pair formation phase preceding egg-laying (Randall and Randall 1981). In all, 42% of the non-breeders observed on a nest were re-sighted as a pair; the remaining birds were recorded either loafing and/or moulting on the nest (Table 4). The values for Areas G and B were 46% and 37% respectively. The sum of the birds recorded in each of these categories exceeds the total number of birds observed on nests, because some of the birds were recorded more than once on a nest and in more than one of the categories during the study.

Birds recovered dead

Of the 2 375 adult *Apollo Sea* birds re-sighted at Dassen Island, 43 (1.8%) were found dead (and reported to SAFRING) by the end of March 2005. Of these, 26 were birds that had been recorded breeding after being de-oiled, and 17 were non-breeders, 1.9% of both the total number of breeders (1 459) and non-breeders (916) that were observed at Dassen Island. Seventeen of the 26 recoveries of breeders (62%) were found at Dassen Island, with 53% of the non-breeders being found there (Table 5). The remaining recoveries of breeders were reported from other penguin colonies in the Western Cape; two from Dyer Island (34°41′ S, 19°25′ E) and one from Bird Island, Lamberts Bay, (32°05′ S, 18°17′ E), one from the penguin colony at Seal Island, Algoa Bay (33°51′ S, 26°16′ E) in the Eastern Cape, and six from non-colony locations in the Western Cape. Nine (53%) of the *Apollo Sea* non-breeder recoveries were reported from Dassen Island, one from the

Table 3: Numbers of de-oiled adult African penguins observed and recorded breeding at Dassen Island per year

Year	Whole island			Study colonies Area G and Area B combined		
	Number observed	Number breeding	Proportion breeding (%)	Number observed	Number breeding	Proportion breeding (%)
1994	307	110	35.8	241	89	36.9
1995	1 649	597	36.2	1 148	506	44.1
1996	1 636	774	47.3	1 123	629	56.0
1997	1 153	488	42.3	844	439	52.0
1998	878	442	50.3	648	390	60.2
1999	700	384	54.9	517	314	60.7
2000	575	304	52.9	451	264	58.5
2001	363	235	64.7	286	195	68.2
2002	288	194	67.4	221	157	71.0
2003	150	93	62.0	116	78	67.2
2004	81	45	55.6	57	34	59.7
2005	13	8	61.5	10	7	70.0

penguin colony at Marcus Island (33°02′ S, 17°58′ E) and the remainder from non-colony locations in the Western Cape (Table 5). All of these non-colony sites were in close proximity to Dassen Island, the farthest being at Grotto Beach, Hermanus (34°25′ S, 19°17′ E), about 160 km from Dassen Island (Figure 1).

Two de-oiled juvenile penguins observed at Dassen Island after release were recovered dead. S22481, released on 21 August 1994, was re-sighted defending a nest with one downy chick on 8 May 1995 (about nine months after having been released as a juvenile). It was observed on five subsequent occasions (never breeding), before being found dead at Dassen Island on 20 March 1997. S22821 was re-sighted on three occasions as a juvenile in 1995, on four occasions as an adult at Dassen Island in 1996 and 1997, four as an adult on Robben Island in 1997, 1998 and 2001, before being found dead at Melkbosstrand (33°43′ S, 18°26′ E), a mainland beach between Robben and Dassen islands, on 10 December 2001. We did not observe the penguin breeding on either island.

Capture-mark-recapture models

Model selection showed that survival in all states, and transition between states, varied over time (Model 2, Table 1 and Figure 7). The best model kept survival for non-breeders and breeders equal, but gave lower survival estimates for secondary non-breeders. The survival difference was constant over time. Transition rates varied over time independently of one another. The probability for non-breeders to start breeding was highest during the early years of the study and then declined (Figure 7b). On average, 31.5% (SE = 2.3) of the breeders became secondary non-breeders each year, and a similar proportion (mean = 29.1%, SE = 3.3) of secondary non-breeders resumed breeding (Figure 7b), implying a constant proportion of secondary non-breeders in the population. However, towards the end of the study the proportion of penguins that stopped breeding increased and the proportion of secondary non-breeders resuming breeding decreased, albeit marginally, implying an increasing proportion of secondary non-breeders at the latter part of the study.

Breeding birds were virtually always detected. Their re-sighting probabilities were 1 and constant over time. On the other hand, the re-sighting probabilities of non-breeders and secondary non-breeders varied over time; secondary non-breeders consistently had a higher re-sighting probability (Figure 7c). This result suggests that similar factors affected movement and behaviour of these two groups. The decline in re-sighting probabilities of non-breeders and secondary non-breeders from 2001 to 2005 (Figure 7c) was due to a reduction in re-sighting effort in coastal surveys during that period. When we used banding at SANCCOB as the first sighting, 11% of the surviving penguins (those penguins re-sighted at Dassen Island at some point during the study period) were found to have resumed breeding in 1994, the same year as they had been oiled (Figure 7b).

The results of the CMR analysis were used to obtain an independent indication of the restoration success of de-oiling penguins following the *Apollo Sea* oil spill. Excluding estimates from the end of the study period, when confidence intervals were large due to a substantially reduced sample sizes, the average annual survival rate for breeders and non-breeders was 0.84, similar to the figure of 0.80 reported

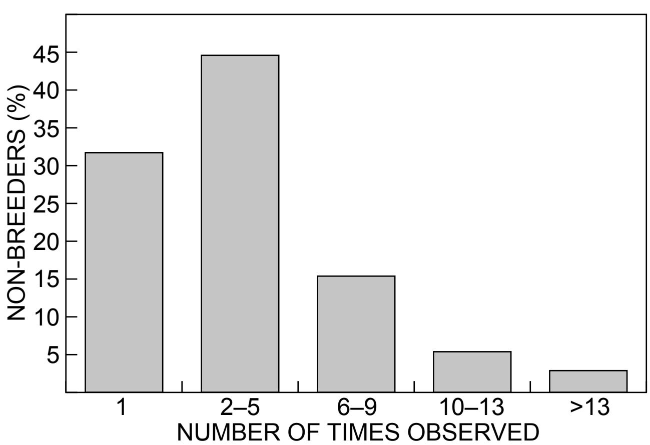

Figure 6: Frequency distribution of the number of times adult African penguins that were oiled in the *Apollo Sea* spill and never recorded breeding again (non-breeders) were observed at Dassen Island

Table 5: Recoveries of dead African penguins involved in the *Apollo Sea* oil spill and observed at Dassen Island after release

Location of recovery	Breeders	Non-breeders
Dassen Island	16	9
Other penguin colonies in the Western Cape	3	1
Other penguin colonies outside the Western Cape	1	0
Non-colony location in the Western Cape	6	7
Total	26	17

Table 4: Number of adult African penguins from the *Apollo Sea* spill that were never recorded breeding, but were observed on a nest at Dassen Island during the period September 1994–March 2005

Parameter	Whole island		Area G		Area B	
	Number of individuals	Number of observations	Number of individuals	Number of observations	Number of individuals	Number of observations
Number of non-breeders re-sighted	916	3 535	297	1 269	184	769
Total observed on a nest	268	368	104	151	75	101
Observed as a 'pair' on a nest	113	135	48	57	28	32
Observed 'loafing' on a nest	153	190	55	71	46	56
Observed 'moulting' on nest	38	41	18	20	12	13

for adult African penguins at Dassen Island by Whittington (2002). Together with the estimates for the probability of transition from non-breeder to breeder each year, these estimates indicate that 73% of the de-oiled birds observed back at Dassen Island attempted to breed. This figure is within the range found in the different study areas on the island by re-sighting methods.

Discussion

Survival of de-oiled penguins compared with oiled birds

Virtually all penguins oiled following the *Apollo Sea* spill were captured alive (Underhill *et al.* 1999). Of the c. 10 000 penguins oiled, 52% died prior to release (Williams 1995a). Half of these deaths resulted from inadequate ventilation while the oiled birds were being transported to SANCCOB. Many of the remaining deaths during de-oiling are attributable to contagious infections, and a lack of understanding at the time of hygiene measures to promote 'herd health' (LGU pers. obs.). Although the original degree of oiling may have been an exacerbating factor in both the major sources of mortality, it seems unlikely that the degree of oiling of penguins that were eventually released differed markedly from the birds that did not survive the rescue and de-oiling process.

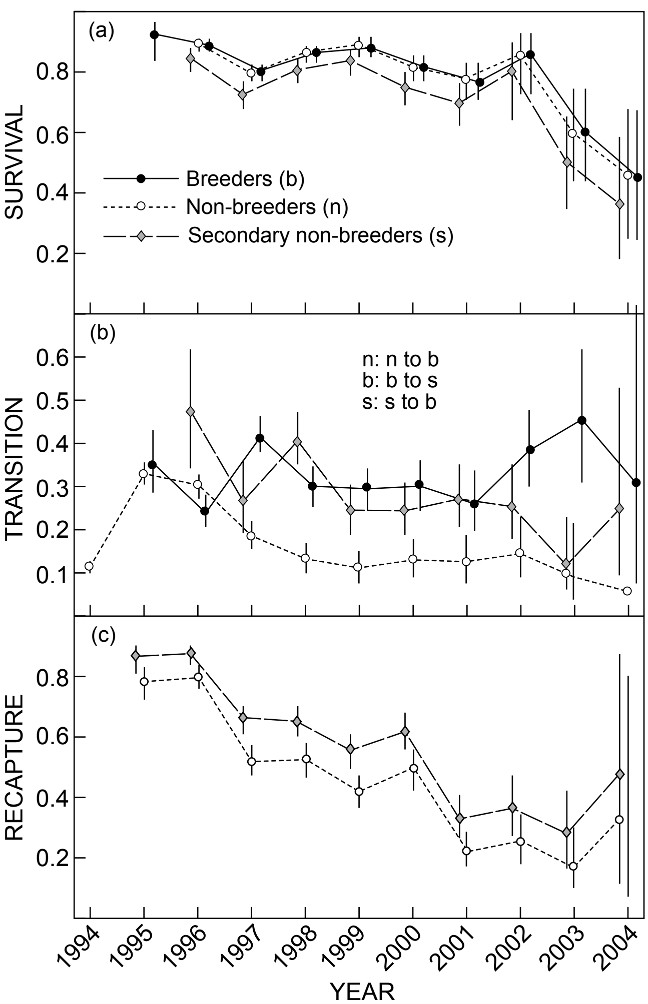

Figure 7: Estimates of (a) survival, (b) transition, and (c) recapture rates of de-oiled African penguins from the *Apollo Sea* oil spill at Dassen Island. The estimates are from Model 2 (see Table 1 and text for details of model selection). The vertical lines show 95% confidence intervals. Recapture rates for breeders were 1 throughout the study. Confidence intervals tend to get larger towards the end of the study because fewer individuals survived that long. The symbols are slightly offset to facilitate comparison

Restoration success

Previous studies have shown that de-oiled African penguins have as good a chance of survival in the wild as birds that have never been oiled (Underhill *et al.* 1999, Whittington 1999b, 2002). Our results show that a substantial proportion of the birds that survived and were re-sighted back at Dassen Island after the *Apollo Sea* oil spill (i.e. rehabilitated) were successfully restored into the breeding population. The proportion of the rehabilitated birds that were recorded breeding was higher for the two study areas (G and B) than for the whole island. This is almost certainly on account of the difficulty of capturing every breeding attempt on the island, where most of the penguins nest in burrows or under boulders, and the more intensive and systematic monitoring of nests in the two study areas. The difference in the proportion breeding between Areas G and B is only marginal and is likely related to the layout of the coast relative to the colony in these two areas. Most penguins that come ashore in Area B breed in the monitored study area, whereas many of the penguins coming ashore along the coast of Area G breed in Areas F and H (ACW pers. obs.; Figure 2), which was not as intensively monitored as Areas G and B, potentially underestimating the proportion of birds observed in Area G that bred. Given that every nest site in the breeding colonies of Areas G and B was checked monthly from November 1994 until the end of 1995, and twice a month from 1996 until March 2005, it is likely that almost all of the birds that bred in these areas would have been detected.

The proportions of de-oiled penguins recorded breeding in this study, whether using the 61% for the whole island or 74% for study Area B, were significantly higher than results previously reported for African penguins. Morant *et al.* (1981) found between zero and 29% (mean = 20%) of the rehabilitated penguins (those seen alive back at their breeding colonies) breeding after seven oiling incidents in the 1970s. The higher proportion recorded breeding in our study is likely to be due to the higher intensity and longer period of monitoring after the *Apollo Sea* spill. It may also be in part because of the enhanced treatment methods at SANCCOB, as reflected by the greatly improved release rates (proportion of oiled birds admitted there that were released in a healthy state) between 1970 and 1994. In the 1970s, the annual average release rate was 52%, increasing to 78% in the 1990s (Nel *et al.* 2003). To the authors' knowledge, this is the first study to assess the restoration success of de-oiled seabirds that spans more than a decade. We are also unaware of any other study of oiled birds that reports such high survival of de-oiled birds to reproduction.

This study focused on the proportion of birds re-sighted at Dassen Island (successfully rehabilitated) that were recorded breeding, rather than the proportion of birds that were released from SANCCOB. The proportion of de-oiled penguins released after the *Apollo Sea* oil spill which 'belonged' to Dassen Island is unknown. The majority (80%) of the oiled birds were removed from Dassen Island, the remainder coming from Robben Island (15%) and other island colonies and mainland beaches (5%) (Dehrmann 1994a, 1994b). However, an unknown proportion of the oiled birds that were removed from Dassen Island may have been birds from other colonies that merely hauled out at the nearest colony (Dassen Island) once they became oiled (Underhill *et al.* 1999), making extrapolations difficult.

Although over 10% of the de-oiled penguins resumed breeding within a year of release, the pattern of cumulative restoration suggests that the rate of restoration was both slower and more sporadic than the rate at which birds were observed for the first time. It also shows that, although the proportion breeding estimates are probably minima, the cumulative totals approached an asymptote two and a half years after the de-oiled birds were released and further monitoring is unlikely to change the proportion breeding results. Indeed, 76% of the adults from Areas G and B that were successfully restored had been recorded breeding by the end of 1996. The slower pattern of restoration relative to the pattern of first re-sightings suggests a slight delay (median interval = 11 months) between the first sighting of the bird back at the colony and its first recorded breeding attempt. This delay may be due to the loss of their mate and the time required to establish a new pair-bond (Fry *et al.* 1986, Kerley and Erasmus 1987, Giese *et al.* 2000) and a disruption of the breeding and moult phenology and synchrony of affected birds (Underhill and Crawford 1999, Hemming 2001, Wolfaardt *et al.* in press a, c). It is also possible that sublethal impacts of ingested oil may have contributed towards physiological impacts which suppressed breeding activities of some individuals temporarily (Butler *et al.* 1988, Walton *et al.* 1997). The step-wise pattern in the rate of cumulative restoration reflected peaks in breeding activity and the time of the annual penguin census, when every active penguin nest was checked for banded birds. The number of 'new' *Apollo Sea* breeders and the gradient of the cumulative restoration graph increased during these periods. Although there appeared to be a slight delay in breeding activities for many of the birds, some individuals were recorded breeding within a month of their release. One bird was observed back at its nest site on Robben Island with two downy chicks a day after it had been released at Silwerstroomstrand (Underhill *et al.* 1999). Its mate was not oiled in the spill and continued rearing the two chicks.

It is not known what proportion of the adult-plumaged penguins released after the *Apollo Sea* spill was of breeding age. Juvenile African penguins moult into adult plumage at an average age 15 months (range 12–23 months) after hatching, about 12 months after fledging (Randall 1989, Kemper and Roux 2005), but generally only start breeding when they are three years or older, with a mean age of first breeding at Dassen Island of 4.6 years (Whittington *et al.* 2005a). This means that some of the birds classified as adults may not have been breeding birds at the time of the spill. However, given the length of the study, and the similar survival rates for birds in their second and subsequent years (Randall 1983, Whittington 2002), the overall results are unlikely to be affected. Further, the oil spill occurred at the peak of the breeding season for African penguins in the Western Cape (Wilson 1985, Crawford *et al.* 1995), so it is likely that the majority of the birds affected would have been breeding adults or birds about to recruit into the breeding population.

It is also possible that a small number of the birds re-sighted at Dassen Island were resident breeders at other colonies. A small percentage (1.9%) of the birds re-sighted at Dassen Island was recorded breeding at other colonies. The majority of these bred at Robben Island, and two at Jutten Island. These are likely to have been transient birds visiting Dassen Island in between breeding activities (Whittington *et al.* 2005c). Eight individual African penguins have been recorded breeding at more than one locality, all of them *Apollo Sea* survivors and all having bred at least once at Dassen Island (Whittington *et al.* 2005b). However, these records are considered to be exceptional, and breeding at more than one colony is an extremely rare event (Randall *et al.* 1987, Whittington *et al.* 2005b). The re-sighting of transient birds at Dassen Island may have introduced some bias to the proportion breeding estimates. If these birds were resident breeders at colonies that received a relatively low level of monitoring, it is possible that breeding attempts by these birds were not detected, thereby underestimating the restoration success. However, given the relatively low incidence of birds moving to colonies other than Robben Island, where observer effort was relatively high, this bias is likely to be minimal.

A minimum of 45% of the birds recorded breeding were still alive and were observed at Dassen Island after five years of release, and 4% were known to have survived into their ninth year. This confirms that the restoration success was not of a short-term nature. Not only were these birds observed alive, but more than half (between 59% and 71%) of the de-oiled *Apollo Sea* adults that were observed each year from 1998 to 2005 were recorded breeding.

The proportion of juvenile birds observed back at Dassen Island and recorded breeding there was lower than that of birds in adult plumage. This is not surprising given that the annual survival rate of African penguins in their first year of life is lower than that of adults (Randall 1983, La Cock *et al.* 1987, Randall 1989, Whittington 2002, but see La Cock and Hänel 1987). Most African penguins start breeding from the age of four or five (Crawford *et al.* 1999, Whittington *et al.* 2005a), reducing further the number of birds that survived until breeding age, and the amount of time available in the study to capture breeding attempts by these birds. The mean estimate for first-year survival of penguins at Dassen Island for the period 1987–1999 was 0.38; survival in subsequent years was 0.80 (Whittington 2002). African penguins breed throughout the year at Dassen Island (Wolfaardt *et al.* in press c), so the juvenile penguins oiled in the *Apollo Sea* spill likely encompass a range of different ages. Using the survival estimates of Whittington (2002) the proportion of de-oiled juveniles surviving to reach five years of age ranges from 54 ($348 \times 0.38 \times [0.80]^4$) if all birds in juvenile plumage were first-year birds to 142 ($348 \times [0.80]^4$) if all birds in juvenile plumage were older than one year. The

22 birds in this group that were recorded breeding represent between 15% and 41% of the birds expected to survive to the age of five. Juvenile African penguins disperse from natal colonies after fledging (Randall *et al.* 1987, Hockey *et al.* 2005), so many of the juvenile penguins oiled in the vicinity of Dassen Island during the *Apollo Sea* spill are likely to have been far away from their natal colony at the time. Of the 10 000 penguins oiled in the *Apollo Sea* incident, 215 were flipper-banded prior to the spill. For those birds whose natal or breeding colony was known, the majority (84%) were from Dassen and Robben islands; for the remainder, the natal or breeding colonies spanned almost the entire range for the species, from Bird Island, Algoa Bay (33°50′ S, 26°17′ E), 730 km to the east, to Ichaboe Island, Namibia (26°17′ S, 14°56′ E), 900 km to the north (Underhill *et al.* 1999, Whittington 2002). In addition, although juvenile African penguins usually recruit to their natal colonies, first-time breeders can recruit to non-natal colonies if food is more plentiful there (Crawford *et al.* 1995, 1999, Crawford 1998, 1999, Whittington *et al.* 2005b). De-oiled juveniles are thus less likely to be observed and recorded breeding than adults, especially if they recruited to colonies that were less intensively monitored.

Non-breeding

A substantial proportion of the de-oiled adult penguins released after the *Apollo Sea* spill resumed breeding, and bred for many years after the spill. However, between 26% and 39% of the de-oiled birds that were successfully rehabilitated (i.e. re-sighted at Dassen Island) never bred again. The case for non-breeding is further supported by multiple observations of many of these birds in the intensively monitored study colonies over long periods of time, some having been re-sighted in 10 of the 12 years of study (1994–2005).

It is possible that some of these birds did breed and their breeding attempts were not detected. Of the non-breeders, 31% were observed only once at Dassen Island. Some of them (9%) were also observed at other breeding colonies (mostly Robben Island), and may have been transient visitors to Dassen Island when re-sighted there. However, a similar percentage (10%) of the *Apollo Sea* breeders was observed 'visiting' other colonies. In both groups, the colony 'visited' on most (>80%) of the occasions was Robben Island, where observer effort was relatively high during the study period, and where most breeding attempts should have been detected (PA Whittington, East London Museum, pers. comm.).

Some of the non-breeders attempted to breed, but were never successful. One-third of them were re-sighted at least once on a nest site, although it is likely that at least some of these birds fled into empty nest sites (in burrows or among boulders) as the observer approached the colony, and were erroneously identified as occupying the nest site. African penguins are vulnerable to disturbance at their breeding colonies (Frost *et al.* 1976, Hockey and Hallinan 1981, van Heezik and Seddon 1990), and penguins loafing at the outskirts of a colony or within it were often observed fleeing away from the observer into nests. Those birds (16% of non-breeders in Area G) re-sighted defending a nest with another penguin (its mate) are unlikely to have been intruders and represent a more accurate reflection of the number of non-breeders attempting to breed. Most of the non-breeders spent little time within the breeding colonies, and were seen more often along the shore, in contrast to breeders that were more likely to be re-sighted within a breeding colony. Similarly, adélie penguin *Pygoscelis adeliae* non-breeders spend fewer days at the rookery than breeders (Ainley *et al.* 1983). African penguins nest in colonies of varying density, with high rates of aggression between adults (Eggleton and Siegfried 1979). For birds that are unable to breed, spending time in a breeding colony may not only be unproductive, but also risky (Renison *et al.* 2002).

It was not possible in this study to compare the de-oiled *Apollo Sea* birds to an un-oiled control group. Large-scale oil spills generate abnormal samples of birds, and it is not possible to establish a proper control group because no group of penguins at colonies is equivalent in terms of age structure and other demographic parameters. Long-term studies of penguins have shown that the proportion of birds breeding varies with age, differs between species, and is dependent on age at first breeding and other life-history parameters (Williams 1995b, Hamer *et al.* 2002, Weimerskirch 2002). The majority of adélie penguins only start breeding from four to six years of age, the proportion increasing to 94% of 12-year-old birds (Ainley 1978). The proportion of adult yellow-eyed penguins *Megadyptes antipodes* breeding reaches its peak at the age of four (Richdale 1957). A long-term study of African penguins at Robben Island found that the most commonly recorded age at first breeding was four, with 80% of known aged birds breeding by Age 6 (Crawford *et al.* 1999). In the latter study, it was thought that birds recorded breeding for the first time at ages older than six had bred earlier without being observed, and so it was assumed that 100% of birds older than four years old were breeders. It is possible that some of the de-oiled *Apollo Sea* non-breeders bred unnoticed, but given the length and intensity of the study, the evidence indicates that oiling inhibited breeding for a proportion (maximum 39%) of the rehabilitated birds.

Sub-lethal impacts of oil contamination

Although we are confident that oiling inhibited breeding for some birds, the mechanisms involved are less certain. Oil contamination has been shown to impact the breeding biology of penguins and other seabirds in a variety of ways. The effects appear to be highly species- and dose-specific. Low levels of oiling of Magellanic penguins *Spheniscus magellanicus* interfered with the circulation of reproductive hormones, which led to lower rates of nest establishment and suppression of egg laying (Fowler *et al.* 1995). Ainley *et al*. (1981) orally dosed cassin's auklets *Ptychoramphus aleuticus* with bunker fuel oil and found that this led to a reduction in the proportion of birds laying eggs, and reduced hatchability in a dose-dependent manner. Similarly, wedge-tailed shearwaters *Puffinus pacificus* exposed both internally and externally to weathered crude oil exhibited progressively reduced breeding with increases in the dosage of oil applied (Fry *et al.* 1986). On the other hand, 0.1 ml of weathered crude oil fed to chicks of fork-tailed storm petrels *Oceanodroma furcata* had little impact on their growth or survival (Boersma *et al.* 1988) Other studies indicate that there is often long-term damage to key organs, especially the liver and kidneys, as a result of the ingestion of even minute quantities of oil (Fry and Lowenstine 1985, Nisbet 1994). Oiled Magellanic penguins have more stomach ulcers and internal parasite loads than un-oiled birds (Gandini *et al.* 1994). Oiling (and handling of birds at rehabilitation centres) may induce immuno-suppressive mechanisms that increase the bird's risk to parasite-mediated infections, as well as reproductive problems (Briggs *et al.* 1996, 1997). Most of the studies reporting sub-lethal effects of oil exposure have focused on the short-term effects of oiling on breeding biology, seldom tracking birds over more than one season. A few studies have followed seabirds over two seasons, with contrasting results. Small doses of oil fed to breeding Leach's storm-petrels *Oceanodroma leucorhoa* resulted in significantly reduced breeding productivity in the season that the birds were oiled, but no effect was detected the following season (Butler *et al.* 1988). On the other hand, Fry *et al.* (1986) reported greatly reduced reproduction in wedge-tailed shearwaters following dosing in the season of treatment, as well as residual effects in the second season that were attributed to the disruption of pair-bonds. Giese *et al.* (2000) found measurable differences in reproductive success in two breeding seasons following the release of de-oiled little penguins after the *Iron Baron* oil spill.

Stress-related suppression of breeding may in part explain the short-term delay in breeding shown by some of the de-oiled *Apollo Sea* birds, but it is unlikely to be the cause of permanent non-breeding. Penguins would likely show lower survival rates if they were exposed to continued stress. Whittington (1999a, 2002) showed that survival rates for de-oiled African penguins are similar to un-oiled birds, and this study reported similar survival rates for *Apollo Sea* breeders and non-breeders, in terms of both the CMR analysis and flipper-band recoveries. It is much more likely then that non-breeding in de-oiled African penguins is related to toxic effects on the reproductive organs, effectively sterilising these birds. The non-breeders may have been the birds that suffered the worst degree of oiling; above a threshold value of oiling (and oil ingestion), the negative impacts of the oil on the reproductive organs may not be possible to reverse through cleaning and treatment. Goldsworthy *et al.* (2000) found that degree of oiling (and its influence on capture mass and body condition) was the most important variable contributing towards the significantly lower survival of de-oiled little penguins, when compared with un-oiled birds, after the *Iron Baron* oil spill. Although the birds were cleaned, treated and released in seemingly healthy condition, birds that experienced lower levels of oiling had the greatest probability of survival, indicating that not all of the deleterious effects of oil contamination were overcome by treatment. Birds in poor condition are known to be more susceptible to the toxic effects of oil than birds in good condition (Fry and Lowenstine 1985). It is likely that the impacts are more complicated than this because the toxic effects of oil may interact synergistically with other stressors (Leighton 1991), such as the capture, handling and treatment of the birds as well as other environmental stressors.

Intermittent breeding and possible costs of reproduction

The relatively high rate at which breeders became secondary non-breeders each year and the lower survival rate of these secondary non-breeders indicates that oiling may have also affected the *Apollo Sea* breeders. In this study, secondary non-breeding refers to non-breeding in birds that had previously bred, which is better termed intermittent breeding to distinguish these birds from the *Apollo Sea* non-breeders. Life-history theory predicts trade-offs between reproduction and survival and between present and future reproduction in a resource-limited environment (Stearns 1976, McNamara and Houston 1996). Several studies of seabirds have found high levels of intermittent breeding (Furness and Monaghan 1987, Chastel *et al.* 1995, Weimerskirch 2002). Some studies have interpreted intermittent breeding as an adaptive strategy to preserve future reproductive value and lifetime reproductive output (Wooller *et al.* 1989, Aebischer and Wanless 1992), whereas others have suggested that intermittent breeding relates to differences in individual quality (Harris and Wanless 1995, Cam *et al.* 1998). The incidence of intermittent breeding at population level is often correlated with environmental conditions, such as weather and food availability (Hays 1986, Crawford and Dyer 1995, Crawford *et al.* 1999, Simeone *et al.* 2002, Crawford 2003). Food availability, and particularly the abundance and distribution of shoaling epipelagic fish (principally anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax*), has been shown to determine the proportion of African penguins breeding each year (Crawford and Dyer 1995, Crawford *et al.* 1999, 2001). At Robben Island, the estimated proportion of experienced adults that did not breed ranged from 30% in 1988 to 0% in 1991 (Crawford *et al.* 1999). At Stony Point (34°22′ S, 18°54′ E), 20% of the total number of breeding attempts possible were missed in the periods 1982–1986 and 1989–1996, 70% of these skipped attempts occurring in years when the colony size was decreasing or when breeding success was low (Whittington *et al.* 1996). The incidence and degree of intermittent breeding of *Apollo Sea* breeders were higher throughout this study compared with the figures reported above for African penguins. Our study took place during a period of significantly increased availability of anchovy and sardine, when rapid increases in the sizes of African penguin breeding colonies in the Western Cape, including Dassen Island, were reported (Wolfaardt *et al.* 2001, Barange *et al.* 2004, du Toit *et al.* 2004, Wolfaardt *et al.* in press a). Increases in the number of African penguins breeding during this period are thought to result from an increased proportion of experienced birds breeding and higher reproductive success (Crawford *et al.* 2006). The relatively high incidence of intermittent breeding for *Apollo Sea* birds during this period is therefore more likely explained by the impacts of oiling on the condition and overall fitness of these birds than by the environmental conditions (food availability) alone.

Further evidence for sub-lethal effects of oiling on the *Apollo Sea* birds is the lower estimated survival rate of secondary non-breeders when compared with both *Apollo Sea* breeders and non-breeders. The negative relationship between breeding and subsequent survival appears to indicate a cost of reproduction for these birds. This is supported by the finding that the proportion of de-oiled *Apollo Sea* birds that stopped breeding increased, and the proportion of the secondary non-breeders resuming breeding decreased, towards the end of the study, suggesting senescence both in survival and reproduction. Due to the moratorium on flipper-banding African penguins, the de-oiled *Apollo Sea* birds could not be compared with an un-oiled control group. Additional support for a cost of reproduction among de-oiled birds is provided by the survivors of the *Treasure* oil spill of 2000. De-oiled birds from the *Treasure* spill had similar survival rates to the un-oiled birds that were evacuated during this spill, until they started breeding, from which point on the survival of de-oiled birds was significantly lower than evacuated (un-oiled) birds (Wolfaardt *et al*. 2008). Dann *et al.* (1995) found no reproductive cost to little penguins in terms of survival or residual reproductive value. In contrast, in a two-year study after the *Iron Baron* oil spill, oiled-rehabilitated little penguins weighed less than non-oiled birds after breeding in both seasons, suggesting that breeding may have exerted a higher energetic cost to oiled-rehabilitated individuals (Giese *et al.* 2000, Goldsworthy *et al.* 2000). Taken together, these results suggest that, despite high post-release survival and restoration success of de-oiled birds, reproduction exacts a higher energetic cost to de-oiled penguins than to un-oiled individuals.

Sex differences

African penguins are difficult to sex visually in the field. In a separate component of this study, individual birds were sexed in order to measure breeding success of de-oiled *Apollo Sea* birds (Wolfaardt *et al.* in press b). However, for the majority of de-oiled birds at Dassen Island, the sexes were not known, and so it is not known whether the effects of oiling were different for males and females. Other studies of penguins have shown that the impacts of oil contamination are greater for females than males. In Magellanic penguins, reduction in body mass and levels of sex hormones, as well as higher levels of corticosterone in oiled females relative to oiled males and un-oiled birds, suggests a higher energetic cost of oiling for females (Fowler *et al.* 1995). Post-release survival of oiled-rehabilitated little penguins is lower in females than males (Goldsworthy *et al.* 2000), and breeding success was found to be lowest in those nests that contained a de-oiled female (Giese *et al.* 2000). It is possible that female African penguins are more susceptible to oil impacts, but we failed to detect a difference in breeding success between *Apollo Sea* birds (Wolfaardt *et al.* in press b).

Conclusion

The findings indicate substantially higher restoration rates than has been previously reported for African penguins (Randall *et al.* 1980, Morant *et al.* 1981), and to our knowledge represent the most successful restoration results for oiled seabirds worldwide. Several factors contribute towards this success, including the robust nature of the African penguin (facilitating their ability to withstand capture and repeated handling), the proximity of the colonies of penguins that were oiled in the *Apollo Sea* spill to the rehabilitation centre, and the relative ease with which flipper-banded penguins can be monitored. Whereas it is clear that the high level of restoration reported justifies the importance of de-oiling African penguins as a conservation management tool, the results show that oil contamination does exert sub-lethal impacts that may reduce long-term reproductive output. Consequently, the conservation status of African penguins would be better served by reducing the occurrence of oil spills in the first place, especially in the vicinity of seabird colonies.

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