

The efficacy of hand-rearing penguin chicks: evidence from African Penguins (*Spheniscus demersus*) orphaned in the *Treasure* oil spill in 2000

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Summary

Some 2,000 orphaned chicks of African Penguins *Spheniscus demersus* were hand-reared and released back into the wild on Robben and Dassen Islands following the *Treasure* oil spill in June 2000. Of these chicks, 1,787 were flipper banded. This paper reports on the subsequent survival rate and breeding success of those individuals seen on Robben Island from 2001–2006. Survival to breeding age and their subsequent breeding success of hand-reared chicks was no different from that of naturally-reared chicks. Over a four-year period, pairs where at least one partner was a hand-reared chick produced an average of more than 1.6 chicks per year. Combining the data on survival with that on breeding success indicates that 1,000 hand-reared chicks will produce around 1,220 chicks themselves over their lifetimes, making this a worthwhile conservation intervention.

Introduction

The raising of young animals for release directly into the wild at an early age of their development can be predicted to have dubious conservation value (e.g. Poulin *et al* 2006, Black 1995, Black *et al.* 1997, Kleiman, 1989). However, there is some evidence that hand-rearing penguin chicks may be a worthwhile conservation intervention. Gildenhuys (1995) described an incident in which African Penguin *Spheniscus demersus* chicks, 'orphaned' by having their parents oiled, were hand-reared to fledging mass and released on Dassen Island. There were indications that many of these orphan chicks survived the critical post-fledging period: none of the 474 hand-reared chicks was recovered dead on Dassen Island, and only six were found dead in the first year after they were released. The youngest of these was two months after release, and the six recoveries were at distances between 191 km and 1,313 km north of Dassen Island (Underhill *et al.* 1999). By 1999, six of the orphaned chicks had been recorded breeding on Dassen Island (Whittington 2002). In 1994, 399 naturally-reared chicks were banded on Dassen Island, five of which have been recorded breeding on the island in the same period (Whittington 2002). Thus, although sample sizes were small, the observed return rates to breed of hand-reared and naturally-reared chicks were similar.

On the strength of this finding, a concerted effort was made to hand-rear African Penguin chicks which were 'orphaned' by the *Treasure* oil spill in June 2000 (Crawford *et al.* 2000). Approximately 3,350 chicks were collected, 2,643 (79%) from Robben Island and the remainder from Dassen Island (Crawford *et al.* 2000). Chicks were collected from all parts of the colonies on

both islands. In total, 1,787 hand-reared chicks were released wearing steel flipper bands (about 500 more were released without flipper bands, and cannot be followed up). Of those released with flipper bands, 732 (41%) were released on Dassen Island and 1,055 (59%) on Robben Island (The South African Bird Ringing Unit, SAFRING *in litt.*). It was not known at which island each chick had been collected, so no attempt could be made to release chicks on their natal island. If the proportions of chicks rescued from each island and ultimately released were similar, and similar proportions were banded, then *c.* 1,410 (79% of 1,787) had been removed from Robben Island.

This paper investigates whether the apparently successful results obtained after the 1994 *Apollo Sea* spill were replicated after the *Treasure* spill. In addition, we evaluate survival rates of hand-reared chicks and compare age at first breeding of hand-reared chicks with naturally-reared chicks.

Methods

Nest monitoring

Between 2001 and 2006, as part of a larger project (e.g. Barham *et al.* 2006, Barham *et al.* 2007), we monitored *c.* 120 African Penguin nests per year on Robben Island (33°49'S 18°22'E), South Africa. Observations covered the main breeding season at this locality, March to August (Crawford *et al.* 1995). The study nests were visited at approximately four-day intervals from hatching to crèching (or death) of the chicks. In addition, incidental observations were made of flipper-banded penguins at nests in the colony as a whole, but only study nests were revisited. In these incidental observations we assumed a bird was breeding only if it was seen in a nest with chicks that were less than three quarters grown or if it was seen feeding a larger chick.

The objective of the main study was to compare the breeding success of three groups of African Penguins in relation to the flipper-banding status: birds fitted with new designs of flipper bands, birds with steel bands and unbanded birds (Barham *et al.* 2007). The study took place in the six breeding seasons which followed the *Treasure* oil spill of June 2000 (Crawford *et al.* 2000), which itself generated three groups of penguins, many of which were banded with steel flipper bands: (1) 17,278 penguins which had been oiled during the spill, rehabilitated and released; (2) 19,506 un-oiled penguins which were removed from the breeding colonies, relocated to Port Elizabeth, Eastern Cape, South Africa, and which swam back to their breeding colonies in the Western Cape while the oil at sea dispersed and the oil on shorelines adjacent to colonies was removed (Crawford *et al.* 2004, Wolfaardt 2004); (3) approximately 2,000 'orphaned' chicks, nestlings whose parents were either oiled, were relocated or abandoned their nests due to the disturbance associated with the rescue operation, and which were hand-reared to fledgling and released, using treatment protocols described by Gildenhuis (1995) and Parsons and Underhill (2005). The third group is the focus of this paper.

One component of the annual fieldwork protocol required the selection of a sample of target size 30–40 study nests at which both adults were already fitted with steel bands. Some of the study nests happened to have pairs in which one of the adults had been a hand-reared chick from the *Treasure* oil spill. We followed the breeding success of these birds as part of the main study. At the time the observations were made, we were not aware that these were hand-reared chicks, so they were not treated in any way different to the remaining study nests.

We used two measures to quantify breeding success: the number of chicks fledged per nest, and the fledgling period. Because we restrict all comparisons to the period between hatching and fledging, it is not necessary to use the Mayfield method to measure success (Mayfield 1975). On each visit to a nest, its contents were checked and the approximate size of chicks was noted. The hatching date of chicks was gauged. We did not weigh chicks, but classified them into five stages of development: P0 newly hatched chicks; P1 small downy chicks; P2 medium to large downy chicks; P3 large downy chicks; P4 chicks with more than half their body covered with final

fledgling plumage, i.e. aged about 45 days or older (Seddon and Van Heezik, 1993). Many surviving chicks eventually joined crèches, when they could not be identified individually as they were not banded. A chick was considered to have fledged if it reached the P₄ stage. Therefore, breeding success may be overestimated. The fledging period was taken as the difference between the date on which a chick was first seen in the nest and the date on which it was last seen at the nest as a P₄ chick. This method will underestimate the actual fledging period. The maximum time between hatching and first observation of a chick in our data is 15 days, although in most cases it is fewer than 5 days. The time between the last sighting of a P₄ chick and its departure to sea is more difficult to estimate.

Estimating survival of hand-reared chicks

We estimated survival of hand-reared chicks using capture-mark-recapture methods (Lebreton *et al.* 1992). These methods correct for the fact that not every individual alive in a given year is observed. The methods assume that, in a given year, every individual has the same probability of surviving and being re-sighted. We anticipated heterogeneity in re-sighting probabilities among individuals because of behavioural differences. For example, some individuals appeared to be active mainly at night, or breed in areas of the island that were not regularly surveyed. Furthermore, young birds and non-breeders may emigrate temporarily to other colonies (Whittington *et al.* 2005c) and then be unobservable. Because of these complications, we used a single simple model where we set the re-sighting rate constant, and allowed survival rates to vary among years. A constant re-sighting rate is justifiable because the field effort varied little among years. However, we corrected the confidence intervals of the estimates for overdispersion using a variance inflation factor and acknowledge that these estimates are preliminary. We estimated overdispersion using a procedure based on Monte Carlo simulation, called the median *c*-hat, in program MARK (White and Burnham 1999). We used MARK to fit the model and estimate parameters.

Results

Between 2001 and 2006, 287 of the 1,787 chicks released with bands (16.1%) were recorded on Robben Island, loafing on the shore, in moult or breeding. Of these birds, 205 (71.4%) had been released on Robben Island and 82 (28.6%) on Dassen Island (Table 1). Thus, of the estimated 1,410 penguins that were originally from Robben Island, 20% were subsequently recorded on Robben Island.

None of the hand-reared chicks was observed attempting to breed on Robben Island during the 2001 breeding season. In the 2002 season, two hand-reared chicks were seen at nests (Table 2). In

Table 1. The number of African Penguins, hand-reared after the *Treasure* oil spill, and re-sighted on Robben Island, 2001–2006. The values are the numbers of different penguins seen in each calendar year. For comparison purposes, the numbers of hand-reared chicks released on Robben and Dassen Islands were 1,055 and 732 respectively.

Year	Number seen on Robben Island	Number seen Robben Island, but released on Dassen Island
2001	193	49
2002	97	34
2003	66	21
2004	53	21
2005	69	23
2006	47	18
Total different birds	287	82

Table 2. The number of nests of African Penguins seen on Robben Island, at which one of the adults had been hand-reared after the *Treasure* oil spill and the outcome of the breeding attempt was known.

Year	Total number of nests	Nests that were followed to completion			
		Nests which failed during incubation	Nests which failed during the pre-fledging period	Nests which fledged one chick	Nest which fledged two chicks
2001	0	0	0	0	0
2002	2	0	0	0	0
2003	19	0	0	1	0
2004	29	2	0	1	1
2005	52	1	1	7	7
2006	26	0	0	3	5

2003, 19 hand-reared chicks were seen at nests with either eggs or chicks (Table 2). One was seen in May with a small chick and again later in July, with a full sized chick close to fledging (Table 2). None of the other nests in these two years was followed to completion of the breeding attempt. In 2004, 29 hand-reared chicks were seen at nests, four of which were followed to completion of the breeding attempt. At these nests the partners of the hand-reared chicks were one bird that had been oiled in the *Treasure* spill, one that had been relocated during the spill, one that had been banded at the Southern African Foundation for the Conservation of Coastal Birds (SANCCOB) following a (minor) oil spill in 1999 and one that was not banded. The fledging success at these four nests was 0.75 fledglings per nest (Table 2). Birds that were oiled in the *Treasure* spill are known to have significantly lower breeding success than other birds (Barham *et al.* 2007), so it is appropriate to discount the nest where the partner of the hand-raised chick was oiled in the *Treasure* spill (which failed to hatch any egg). In this case the rate becomes 1.0 fledglings per nest.

In 2005, 52 hand-reared chicks were observed at nests, five of which were followed to the outcome of the breeding attempt. In addition, we saw parents that had been hand-reared as chicks with near fully grown chicks (at P₃ to P₄ stage) at a further 11 nests and concluded, on the basis of the very low mortality of chicks once they are well into the P₃ stage reported elsewhere (Barham *et al.* 2007), that chicks were successfully raised at these nests (Table 2). The success rates at the five study nests were 1.2 chicks per nest or 1.5 chicks per nest where eggs hatched. If we discount two nests where the hand-reared chicks were partnered by a bird oiled in the *Treasure* oil spill (at one no eggs hatched and at the other both chicks died when approximately half grown) the rate became 2.0 chicks per nest where eggs hatched.

In 2006, 26 hand-reared chicks were observed at nests, three of which were followed to their outcomes. In addition, we saw parents that had been hand-reared as chicks with near fully grown chicks at a further five nests and concluded that chicks were successfully raised at these nests (Table 2). The success rates at the three study nests were 1.7 chicks per nest.

Overall the breeding success rate of the hand-reared chicks appears to be at least as good as, if not better than, that of naturally reared chicks. Over the three years from 2004 to 2006, naturally reared birds (that were not oiled in the *Treasure* spill) have raised an average of 1.1 chicks per pair ($n = 227$) (Barham *et al.* 2007, unpublished data for 2006) compared to an average of 1.6 chicks per pair ($n = 24$) for the hand-reared chicks (excluding those partnered by a bird that was oiled in the *Treasure* spill). The sample size is too small to determine whether the difference is significant.

In total, these breeding observations refer to 97 individual birds, 23 of which were recorded breeding in more than one year. These birds correspond to 5.4% of all the hand-reared *Treasure* chicks, and 6.8% of the total number (1,410) we estimated 'belong to' Robben Island. Because we

monitored only a fraction of all breeding attempts by banded birds on Robben Island, the 97 individual penguins represent the minimum number breeding, and the true total is likely to be several times larger. The 97 penguins confirmed as breeding on Robben Island constitute 34% of the total number of hand-reared penguins (287) seen on Robben Island during the study.

The mean age (taken from the date of release when the birds were about four months old on average) at which these chicks were first seen breeding was 4 years 2 months ($n = 97$, $SD = 10$ months). The minimum age at first breeding was 1 year 9 months, and the minimum age at which the breeding attempt was known to be successful was 2 years 10 months.

Survival rates of hand-reared chicks

The estimated overdispersion for the model used to estimate survival rates (Figure 1) was 1.38 ($SE = 0.04$) and we used this estimate as a variance inflation factor. The model recapture rate for the study period was 0.21 (95% confidence interval 0.17 to 0.25).

Our methods for estimating survival cannot distinguish between mortality and permanent emigration, and the survival estimates for 2000 and 2001 are therefore almost certainly biased low since birds that emigrated are assumed to have died. Casual observations have shown that there are at least 3 of the hand-reared chicks breeding elsewhere (2 at Boulders and 1 at Stoney Point) with a further 4 having been seen at these locations in the past two years (PJB pers. obs.).

Discussion

These results confirm the finding of Whittington (2002) that hand-reared chicks of African Penguins have reasonable survival in the wild. They endorse the conservation recommendations implicit in Whittington (2002): (1) in future oil spills, chicks of oiled parents can be hand-reared successfully to fledging and released; these fledglings are as fit as naturally-reared chicks; (2) in spite of this, if resources are scarce, priority should be given to de-oiling breeding adults, because their residual fitness exceeds that of chicks.

The second recommendation remains valid even in the light of the recent finding that the residual fitness of a de-oiled penguin from the *Treasure* spill is less than that of a never-oiled bird (Barham *et al.* 2007, Wolfaardt 2007). Our results here suggest that, of 1,000 hand-reared female chicks, approximately 135 survive to breeding age. This is based on survival rates in the first four years (Figure 1). Assuming a productivity of 1.63 fledglings per female per year, the mean productivity in the years 2002–2006, these females would produce approximately 220 chicks in their first year of breeding, decreasing by 18% per year through natural mortality,

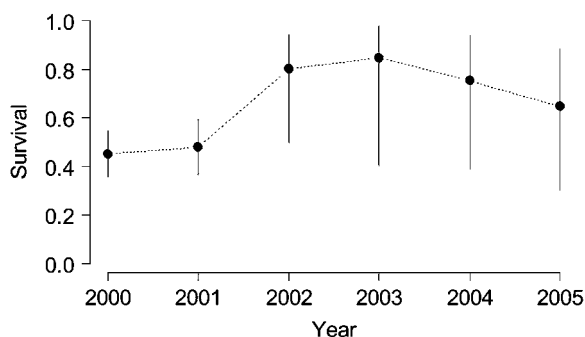


Figure 1. Annual survival rates of hand-reared African Penguin chicks on Robben Island from 2000 to 2005. The vertical lines show 95% confidence intervals. Estimates for 2000 and 2001 are almost certainly underestimates (see text).

using a survival rate of 82% (Crawford *et al.* 1999), to produce an estimated 1,220 chicks in their lifetimes, effectively replacing themselves. The results of Wolfaardt (2007) suggest that, of 1 000 de-oiled female adult penguins, about 26% do not breed again. Those that do breed, produce 460 chicks per year, based on a productivity of 0.63 chicks per female per year for de-oiled *Treasure* females from 2002–2006 on Robben Island (Barham *et al.* 2007, unpubl. data for 2006). The estimated lifetime production of these birds, applying a similar survival rate, is 2,555 chicks. Thus, in spite of the impact of oil on the breeding performance of penguins, de-oiling of adults has a conservation significance about double that of hand-raising chicks. It should be borne in mind that birds oiled in the *Treasure* spill had a poorer breeding performance than penguins oiled in other spills, perhaps because of the long period they were held before being de-oiled (Barham *et al.* 2007). Most African Penguins breed for the first time when about four years old (Whittington *et al.* 2005a), but results presented here indicate some are clearly capable of breeding at a younger age.

Hand-reared chicks have two potential advantages over naturally reared chicks, although whether either of these is valid remains to be tested. Firstly, hand-reared chicks invariably are released in excellent condition, at above the average fledging mass. On average they spend 65 days at SANCCOB, the penguin rescue centre in Cape Town, before release, so they are about a month older than naturally-reared fledglings when released (Parsons and Underhill 2005). Secondly, unlike naturally-reared fledglings, they have extensive swimming experience when they go to sea for the first time. Provided they are in good condition, they swim daily in a large fresh water pool at the penguin rescue centre (N. J. Parsons *in litt.*). A disadvantage of releasing hand-reared chicks is the risk of introducing diseases into the wild population.

Besides being a consequence of oiling events, there are two further contexts in which penguin chicks may be “orphaned”: (1) at certain penguin colonies, a number of chicks at all stages of development are abandoned each year when their parents enter moult; (2) many zoos and aquaria have displays of African Penguins, and the offspring of these captive penguins are potentially available to bolster the wild population.

Chicks are abandoned in colonies at the commencement of the main moult season at, for example, Robben Island, Boulders and Dyer Island (Parsons and Underhill 2005, RJMC, LGU pers. obs; L.J. Waller *in litt.*). In 2001 and 2002, two years in which there were no major oil spills, the numbers of abandoned chicks admitted to SANCCOB were 82 and 96, respectively (Parsons and Underhill 2005). In November 2006, c. 700 abandoned chicks were admitted to SANCCOB from Dyer Island, coinciding with the commencement of the timing of peak moult on this island (L.J. Waller *in litt.*). As these chicks would die without intervention, the rescue and hand-rearing of such chicks is a valid conservation action and if carried out each year should augment the future breeding population. The disturbance involved in collecting chicks that have become orphaned following oil spills or for other reasons is an important factor to consider in such operations. Shannon and Crawford (1999) raised concern about the long-term impact of the disturbance associated with searching for and collecting oiled penguins on African Penguin colonies. For large scale incidents, this is likely to be less of an issue because of the rescue activities that would already be underway (but should still be conducted in a manner that minimises disturbance), but for ongoing chronic oiling, and the desertion of nests by only some penguins, activities need to be planned and conducted so as to minimise disturbance.

Interventions to bolster failing populations of threatened birds are becoming increasingly common. Examples involving rearing chicks for release include the Southern Ground Hornbill *Bucorvus leadbeateri* in South Africa (Kemp 1995) and a number of passerine species on Mauritius (Wilkinson 2006). Eggs and/or chicks are removed from the nest, hand-reared to fledging using expertise developed with similar species in captivity, and released back into the wild population once independent.

One of the stated objectives of many zoological gardens, especially those in Europe and North America, is that the offspring of their captive animals could be used to bolster wild populations, especially of species that are likely to become extinct without the intervention of intensive

management techniques developed for birds in captivity (e.g. Black 1995, Black *et al.* 1997, Jones and Swinnerton 1997, Safford and Jones 1998, Garnet and Crowley 2000, Swinnerton 2001).

Because hand-reared African Penguin chicks are as fit as naturally-reared chicks, the species is a particularly promising candidate for a captive-breeding programme which aims to release offspring into the wild. Many zoological gardens and aquaria in Europe and North America have African Penguins in their collections and the species breeds readily and productively in captivity. In fact, there is surplus production, the chicks have little commercial value in trade between facilities and African Penguins are discouraged from breeding to avoid overcrowding (DAB pers. obs). In North America, a breeding embargo within the managed programme was imposed for a number of years and in Europe breeding has been slowed down at the request of the species management committee. These populations could be allowed to breed unrestricted to produce young for release into the wild.

Before a large-scale project to bolster wild African Penguin populations from captive-bred birds is initiated two issues need to be resolved: (1) the potential for introducing new diseases into wild populations; (2) an understanding of mechanisms that lead to most African Penguin fledglings returning to their natal colonies to breed.

For African Penguins, there are particular concerns about the introduction of new strains of avian malaria from Europe and North America. The overwhelming majority of African Penguins return to their natal islands to breed (Whittington *et al.* 2005b). It is not known at what age penguins develop this knowledge of the location of their natal island. If it is at the time of fledging, then the release site of hand-reared chicks may provide this cue. The only way in which to learn about these issues and understand whether captive breeding programmes can make a contribution to bolstering African Penguin populations is through careful experimentation. Such experiments would not only have conservation significance; they could also provide valuable insights into our understanding of orientation in animals in general.

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References

- Barham, P. J., Crawford, R. J. M., Underhill, L. G., Wolfaardt, A. C., Barham, B. J., Dyer, B. M., Leshoro, T. M., Meÿer, M. A., Navarro, R. A., Oschadleus, H. D., Upfold, L., Whittington, P. A. and Williams, A. J. (2006) Return to Robben Island of African Penguins that were rehabilitated, relocated or reared in captivity following the *Treasure* oil spill of 2000. *Ostrich* 77: 202–209.
- Barham, P. J., Crawford, R. J. M., Underhill, L. G. and Leshoro, T. M. (2007) Differences in breeding success between African Penguins that were and were not oiled in the *Treasure* oil spill in 2000. *Emu* 107: 7–13.

- Black, J. M. (1995) The Nene *Branta sandvicensis* recovery initiative: research against extinction. *Ibis* 137 (Suppl. 1): S153–S160.
- Black, J. M., Marshall, A. P., Gilburn, A., Santos, N., Hoshide, H., Medeiros, J., Mello, J., Natividad Hodges, C. and Katahira, L. (1997) Survival, movements, and breeding of released Hawaiian Geese: an assessment of the reintroduction program. *J. Wildl. Manage.* 61: 1161–1173.
- Crawford, R. J. M., Boonstra, H. G. v. D., Dyer, B. M. and Upfold, L. (1995) Recolonization of Robben Island by African Penguins, 1983–1992. Pp. 333–363 in P. Dann, I. Norman and P. Reilly, eds. *The penguins: ecology and management*. Chipping Norton, Australia: Surrey Beatty.
- Crawford, R. J. M., Davis, S. A., Harding, R., Jackson, L. F., Leshoro, T. M., Meÿer, M. A., Randall, R. M., Underhill, L. G., Upfold, L., van Dalsen, A. P., van der Merwe, E., Whittington, P. A., Williams A. J. and Wolfaardt, A. C. (2000) Initial impact of the *Treasure* oil spill on seabirds off western South Africa. *S. Afr. J. Mar. Sci.* 22: 157–176.
- Crawford, R. J. M., Meÿer, M. A., Underhill, L. G. and Upfold, L. (2004) Relocation of African Penguins to prevent their becoming oiled after the sinking of the *Treasure*, and the tracking of their return. Pp. 13–16 in S. Kuyper and A. J. Williams, eds. *Proceedings of the penguin workshop following the sinking of the Treasure in June 2000*. Cape Town: Avian Demography Unit, University of Cape Town.
- Crawford, R. J. M., Shannon, L. J. and Whittington, P. A. (1999) Population dynamics of the African Penguin *Spheniscus demersus* at Robben Island, South Africa. *Mar. Ornithol.* 27: 139–147.
- Garnett, S. T. and Crowley, G. M. (2000) *The action plan for Australian birds 2000*. Canberra: Environment Australia.
- Gildenhuis, A. (1995) Capture, care and release of orphaned African Penguin chicks at Dassen Island. Pp. 18–20 in J. Barrett, Z. Erasmus and A. J. Williams, eds. *Proceedings coastal oil spills: effects on penguin communities and rehabilitation procedures*. Cape Town: Cape Nature Conservation.
- Jones, C. G. and Swinnerton, K. J. (1997) A summary of the conservation status and research for the Mauritius Kestrel *Falco punctatus*, Pink Pigeon *Columba mayeri* and Echo Parakeet *Psittacula eques*. *Dodo (J. Jersey Wildl. Preserv. Trust)* 33: 72–75.
- Kemp, A. C. (1995) *The Hornbills: Bucerotiformes*. Oxford: Oxford University Press.
- Kleiman, D. G. (1989) Reintroduction of captive mammals for conservation. *Bioscience* 39: 152–161.
- Lebreton, J. D., Burnham, K. P., Clobert, J. and Anderson, D. R. (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* 62: 67–118.
- Mayfield, H. F. (1975) Suggestions for calculating nest success. *Wilson Bull.* 87: 456–466.
- Parsons, N. J. and Underhill, L. G. (2005) Oiled and injured African Penguins *Spheniscus demersus* and other seabirds admitted for rehabilitation in the Western Cape, South Africa, 2001 and 2002. *Afr. J. Mar. Sci.* 27: 289–296.
- Poulin, R. G., Todd, L. D., Wellicome, T. I. and Brigham, R. M. (2006) Assessing the feasibility of release techniques for captive-bred burrowing owls. *J. Raptor Res.* 40: 142–150.
- Safford, R. J. and Jones, C. J. (1998) Strategies for land-bird conservation on Mauritius. *Conserv. Biol.* 12: 169–176.
- Seddon, P. J. and van Heezik, Y. M. (1993) Behaviour of the Jackass Penguin chick. *Ostrich* 64(1): 8–12.
- Shannon, L. J. and Crawford, R. J. M. (1999) Management of the African Penguin *Spheniscus demersus* – insights from modelling. *Mar. Ornithol.* 27: 119–128.
- Swinnerton, K. (2001) Ecology and conservation of the Pink Pigeon *Columba mayeri* on Mauritius. *Dodo (J. Jersey Wildl. Preserv. Trust)* 37: 99.
- Underhill, L. G., Bartlett, P. A., Baumann, L., Crawford, R. J. M., Dyer, B. M., Gildenhuis, A., Nel, D. C., Oatley, T. B., Thornton, M., Upfold, L., Williams, A. J., Whittington, P. A. and Wolfaardt, A. C. (1999) Mortality and survival of African

- Penguins *Spheniscus demersus* involved in the *Apollo Sea* oil spill: an evaluation of rehabilitation efforts. *Ibis* 141: 29–37.
- White, G. C. and Burnham, K. P. (1999) Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46: S120–139.
- Whittington, P. A. (2002) Survival and movements of African Penguins, especially after oiling. PhD thesis, University of Cape Town, South Africa.
- Whittington, P. A., Klages, N. T. W., Crawford, R. J. M., Wolfaardt, A. C. and Kemper, J. (2005a) Age at first breeding of the African Penguin. *Ostrich* 76: 14–20.
- Whittington, P. A., Randall, R. M., Crawford, R. J. M., Wolfaardt, A. C., Klages, N. T. W., Randall, B. M., Bartlett, P. A., Chesselet, Y. J. and Jones, R. (2005b) Patterns of immigration to and emigration from breeding colonies by African Penguins. *Afr. J. Mar. Sci.* 27: 205–213.
- Whittington, P. A., Randall, R. M., Randall, B. M., Wolfaardt, A. C., Crawford, R. J. M., Klages, N. T. W., Bartlett, P. A., Chesselet, Y. J. and Jones, R. (2005c) Patterns of movements of the African Penguin in South Africa and Namibia. *Afr. J. Mar. Sci.* 27: 215–229.
- Wilkinson, R. (2006) Hornbills - their captive management and in-situ conservation. Pp. 11–12 in B. Hiddinga and R. de Jong, eds. *Proceedings Special Edition, EAZA Symposium 2006 on the occasion of Koen Brouwer's farewell to the EAZA Executive Office*. Amsterdam: EAZA Executive Office.
- Wolfaardt, A. C. (2004) The capture and removal of clean penguins from Dassen Island. Pp. 8–13 in S. Kuyper and A. J. Williams, eds. *Proceedings of the Penguin Workshop following the sinking of the Treasure in June 2000*. Cape Town: Avian Demography Unit, University of Cape Town.
- Wolfaardt, A. C. (2007) The effects of oiling and rehabilitation on the breeding productivity and annual moult and breeding cycle of African Penguins. PhD thesis, University of Cape Town, South Africa.

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