

# Artificial nests enhance the breeding productivity of African Penguins (*Spheniscus demersus*) on Robben Island, South Africa

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**Abstract.** Loss of nesting habitat threatens many cavity nesting birds worldwide and has contributed to the decline of several species of burrow-nesting seabirds. Replacing lost habitat with artificial nesting structures is considered to be a useful conservation intervention. Here we report on an investigation into the effectiveness of such a strategy – providing artificial nests for the endangered African Penguin (*Spheniscus demersus*) at a colony on Robben Island, South Africa. The re-colonisation of Robben Island by breeding African Penguins in the 1980s was partly attributed to the availability of shaded nesting habitat under introduced vegetation. However, the suitability of this habitat had not been tested empirically. In addition, artificial nests have been present at Robben Island since 2001, but whether they were a viable means of providing improved nesting habitat was not known. The reproductive output of African Penguins was monitored on Robben Island from 2001 to 2010. Breeding success varied between years but, overall, was within the range of figures previously reported for the species. Relative to pairs in nests under vegetation, birds occupying artificial nests and nests in abandoned buildings had increased nesting survival during chick-rearing, with 9 and 13% more chicks fledged per egg hatched over the study period. These artificial structures seem to offer the advantages of shelter from the weather and protection from predators, without the risks of collapse associated with natural burrows in non-guano substrates. This study supports findings from Namibia, and also supports the continued use of artificial nests as a conservation tool throughout the range of the species.

**Additional keywords:** breeding success, burrow-nesting seabirds, nesting habitat loss, nest-boxes, nest-sites, nesting success, penguin conservation.

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## Introduction

The loss and modification of breeding habitat are considered to be major threats to global avian biodiversity (Gaston *et al.* 2003). Many avian orders have evolved life-history or phenotypic traits that tie them to nesting in some form of cavity, with the result that their populations can undergo dramatic declines if suitable nesting sites become scarce (e.g. Newton 1994). Through the removal of suitable burrowing substrate, the large-scale collection of guano deposits along the coasts of South America and southern Africa since the mid-19th century are thought to have contributed to large historic population decreases of several seabirds evolved to nest in holes (e.g. Duffy *et al.* 1984; du Toit *et al.* 2003),

including globally threatened species such as the Humboldt Penguin (*Spheniscus humboldti*; Hays 1984) and African Penguin (formerly Jackass Penguin, *Spheniscus demersus*; Frost *et al.* 1976b). The *Spheniscus* penguins are temperate to tropical in their distribution, but they are adapted to forage in cold water so can become heat stressed on land (Frost *et al.* 1976a). As a result, *Spheniscus* penguins preferentially use nesting sites where they can avoid direct solar radiation (Frost *et al.* 1976a; La Cock 1988; Stokes and Boersma 1998) and breed more successfully in nesting sites with cover relative to those in the open (e.g. Frost *et al.* 1976b; Stokes and Boersma 1998; Paredes and Zavalaga 2001). Historically, African Penguins principally dug burrows

into the hard guano layer that covered most breeding islands in southern Africa (Frost *et al.* 1976a, 1976b). However, in the absence of the guano, these birds must breed in a variety of suboptimal habitats, including on the surface (Frost *et al.* 1976b; Wilson and Wilson 1989).

In 2011, the African Penguin is classified as endangered (BirdLife International 2010) and the species exhibits high spatial and temporal variation in breeding success (e.g. Crawford *et al.* 2006). Although this is primarily thought to be driven by the availability of food (e.g. Durant *et al.* 2010), other factors have been identified that influence productivity, including the type and quality of nest (see e.g. Frost *et al.* 1976b; Seddon and van Heezik 1991; Kemper *et al.* 2007a, 2007b), stochastic weather events (Seddon and van Heezik 1991; Kemper *et al.* 2007b) and predation of eggs and chicks (e.g. Seddon and van Heezik 1991; Crawford *et al.* 1995b). African Penguins nesting on the surface may abandon their nests when it is excessively hot to go to sea to cool down, leaving the nest contents vulnerable to predation (Randall 1995), and burrows in unsuitable substrates can collapse or flood following heavy rain (Seddon and van Heezik 1991). Where possible, replacing lost nesting habitat with artificial structures is often considered to be an important conservation intervention (see e.g. Newton 1994; Lambrechts *et al.* 2012). Consequently, artificial nests for African Penguins have been used with some success at Marcus Island, in Saldanha Bay, South Africa (Wilson and Wilson 1989) and Halifax Island in Namibia (Kemper *et al.* 2007b). Given the decline in the population during the first decade of the 21st century, and the conservation status of the species (Crawford *et al.* 2011), concerted efforts have been made to increase survival and reproductive success in recent years. As a result, large numbers of artificial nests have been placed on Dyer Island and Boulders Beach, Western Cape, South Africa (L. J. Waller, pers. comm.) and Bird Island, Algoa Bay, Eastern Cape, South Africa (Pichegru, *in press*) in the last few years with the aim of improving the breeding habitat available to African Penguins. It is the primary purpose of this study to determine the effectiveness of such interventions using a long-term dataset from a colony on Robben Island, South Africa.

African Penguins began nesting again on Robben Island, in South Africa's Western Cape, in 1983, after 180 years of absence caused by human disturbance (Shelton *et al.* 1984). On Robben Island, most nests are shallow scrapes dug beneath introduced vegetation, predominately Rooikrans (*Acacia cyclops*) and Manatoka (*Myoporum tenuifolium*). However, the Penguins also dig burrows in sandy soil, occasionally dig scrapes in the open and nest in old disused buildings or under discarded artificial materials. It has been suggested that the availability of sheltered sites under introduced vegetation was one of the factors contributing to the re-colonisation of the island (Crawford *et al.* 1995b). Consequently, the initiation of a widespread program of clearing of introduced trees by the managing authority of Robben Island (Robben Island Museum 2006) prompted the installation of purpose-made artificial nesting boxes (made of plywood) and, later, artificial burrows (made of fibreglass). A number have now been occupied on Robben Island since 2001. Improving breeding success, including by maintaining or improving breeding habitat, has been identified as one of the key conservation actions needed to address the decline of the African Penguin (BirdLife Interna-

tional 2010). Provision of custom-made artificial nests could assist with improving breeding success at many colonies, provided that their efficacy can be shown and thus that the cost and action of providing them can be justified. This paper describes a study undertaken to determine the breeding productivity of African Penguins on Robben Island over 10 years in the different types of nest available on the island. We investigate whether the custom-made artificial nests have provided adequate nesting habitat and thus could be a viable option in the event of widespread clearance of introduced vegetation on Robben Island or at other colonies where vegetation is largely absent. Based on the findings of Kemper *et al.* (2007a) on Halifax Island, we expected the artificial nests to improve brood survival compared with scrapes in the open and nests under vegetation (Kemper *et al.* 2007a). However, African Penguins on Robben Island can potentially lose eggs and chicks to predation (e.g. Underhill *et al.* 2009), so we also compared nesting success during the incubation period and measures that provide an index of the loss of single eggs or chicks.

## Methods

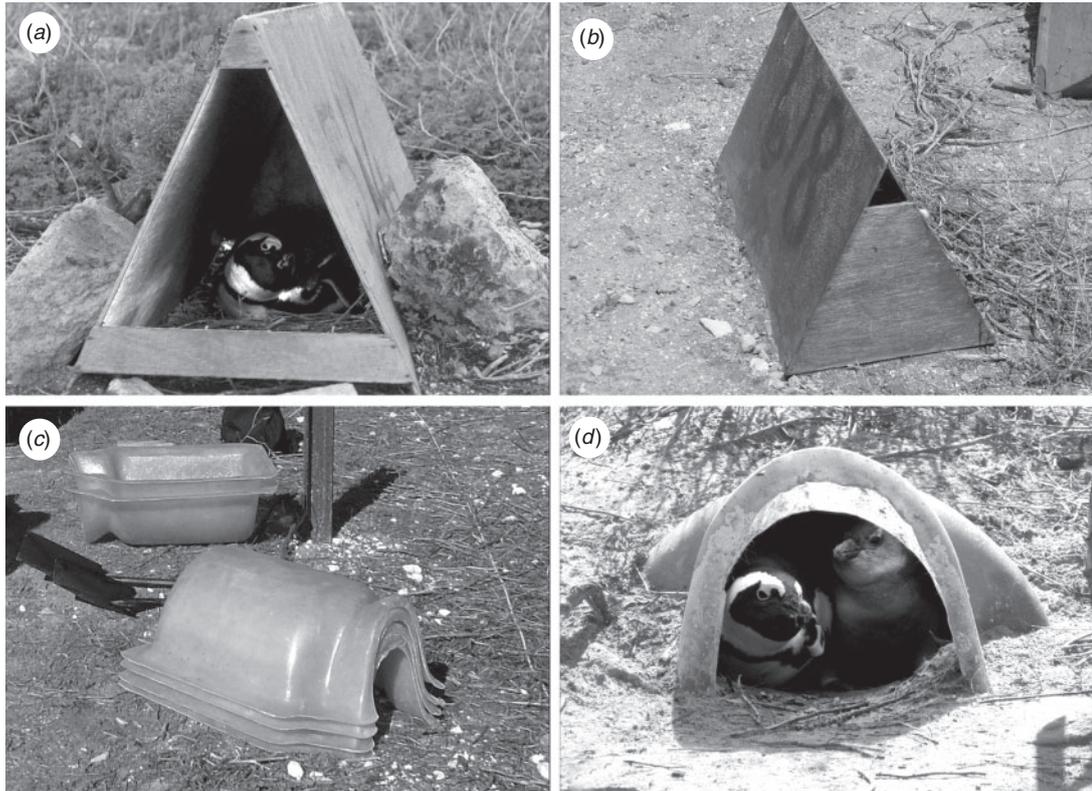
### *Study site and species*

The study was conducted in the African Penguin colony on Robben Island (33°48'S, 18°22'E) over 10 breeding seasons (2001–10). Robben Island was declared a global Important Bird Area in 1998 (Barnes 1998) and a Cultural World Heritage Site by UNESCO in 1999 (World Heritage Committee 2000). At the start of the study, Robben Island supported the third largest colony of African Penguins, with ~6700 breeding pairs (Underhill *et al.* 2006; Crawford *et al.* 2011). During the 10 years of monitoring, the population increased to a peak of ~8500 pairs in 2004 (Underhill *et al.* 2006) but then declined to ~2500 breeding pairs by 2010 (Crawford *et al.* 2011).

African Penguins show peaks of breeding specific to localities and regions (e.g. Crawford *et al.* 1995c; Kemper *et al.* 2007b). In the Western Cape, breeding predominately occurs during the austral winter (Crawford *et al.* 1995c). On Robben Island, between 1989 and 1995, 85% of first clutches were laid between February and May and 85% of clutches consisted of two eggs (Crawford *et al.* 1999). Clutch-size ranges from one to (rarely) three eggs, with the mean usually ~1.8 (e.g. Crawford *et al.* 1999; Kemper *et al.* 2007b). Second clutches are laid both after failure (at the egg and chick stages) and after successful attempts, but third clutches are rare (Crawford *et al.* 1999). Second clutches can be successful in some cases (La Cock and Cooper 1988). Breeding success varies, with two chicks fledged in 43–64% of successful attempts (e.g. Barham *et al.* 2007; Kemper *et al.* 2007b; Sherley 2010), after a hatching–fledging period of 60–130 days (Cooper 1980; Randall 1995).

### *Design of artificial nests*

Custom-made artificial nests of two different designs were available to breeding Penguins on the island during the study. In 2001, 22 artificial nest-boxes were set up on the island by staff of the Department of Environmental Affairs (then the Department of Sea Fisheries). These were free-standing wooden structures made of 3-mm-thick pine plywood, varnished on the outer surface. The boxes were a triangular prism (see Fig. 1a, b), formed from two



**Fig. 1.** Examples of the two custom-made artificial nests monitored for African Penguin breeding success and nest survival on Robben Island from 2001 to 2010. The plywood boxes, shown from the front (a) and rear (b), were first placed on the island in 2001. The fibre-glass artificial burrows, shown before they were dug in (c) and once installed and occupied (d), were first used in 2007. The wooden boxes and artificial burrows were combined under the category ‘Artificial Nest’ for analysis (see Tables 1, 2).

panels measuring 790 mm long by 430 mm high to form the sides and a triangular panel measuring 380 mm high by 380 mm wide to form the rear of the box, giving a floor space of 0.3 m<sup>2</sup>. An opening (~70 mm high by 90 mm wide) was left near the top rear of the box to allow for ventilation (Fig. 1b). The front of the box was reinforced with a piece of wood 380 mm long (across the base of the entrance), but otherwise left open (Fig. 1a). The first breeding attempt in a wooden box was recorded in April 2001. An additional 37 nest-boxes were provided in 2005, and 10 more in 2010. Several of the original boxes had begun to deteriorate and were replaced in 2010 with slightly larger boxes of the same design.

In May 2007, 70 artificial burrows (Fig. 1c, d) were placed on Robben Island by the authors (RBS, BJB and TML) and several volunteers. The burrows were designed and manufactured from fibreglass and resin mesh by the Dyer Island Conservation Trust (<http://www.dict.org.za/>) with the aim of closely mimicking the shape of a natural African Penguin burrow (B. Walters, pers. comm.). The burrows (see Fig. 1) measured 600 long and 400 mm wide at their base, giving an approximate floor space of 0.24 m<sup>2</sup>, and were 300 mm high. The thickness of the walls varied (they were hand-made) but was ~3 mm. The burrows were initially dug into the ground, leaving an opening ~25 mm wide (at the base) and 28 cm high. The floor of the burrows (and the wooden boxes) was open (see Fig. 1c) to allow water to drain away and to allow the occupants to dig. Thus, the internal space available to the birds

often differed between nests. The artificial burrows were initially covered with rocks and soil, but this covering only remained to a varying degree in most cases as a result of wind and rain (Fig. 1d).

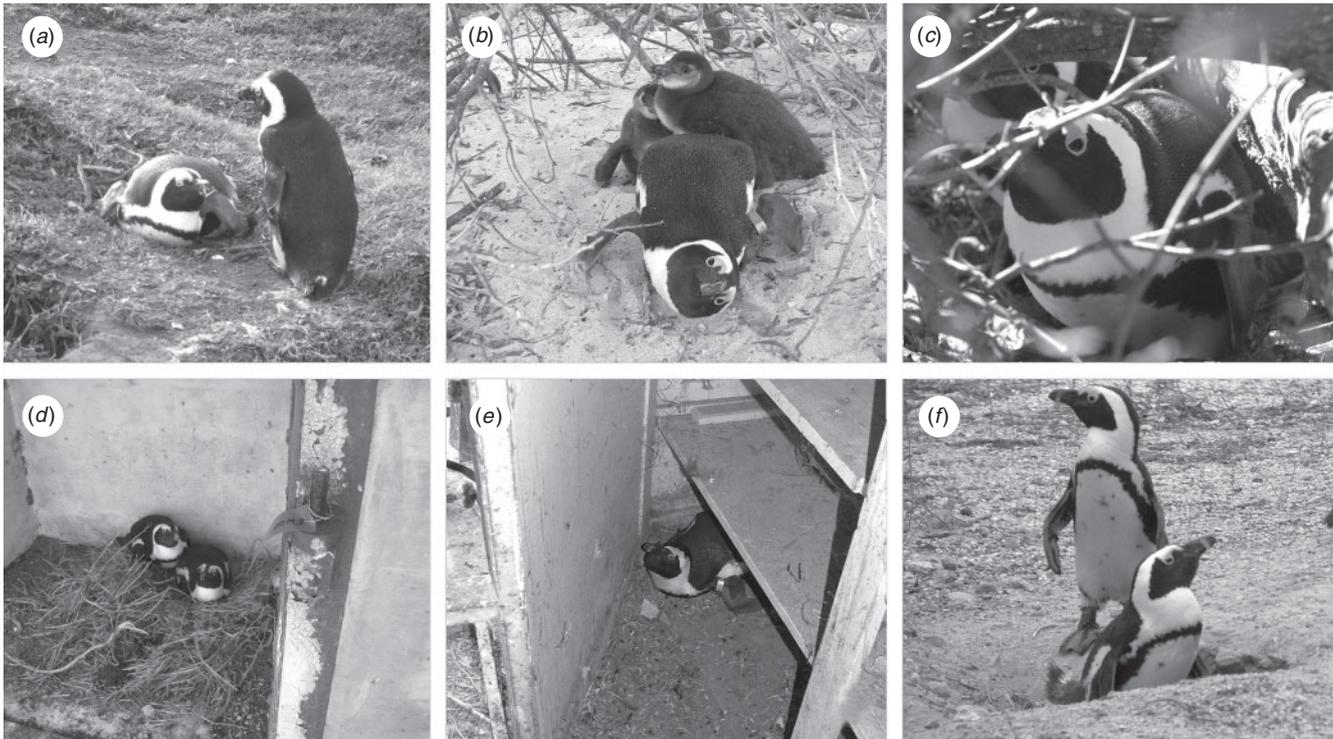
#### Monitoring of nests

As part of a larger project (e.g. Crawford *et al.* 2006; Barham *et al.* 2007; Sherley 2010), we monitored between 70 and 274 African Penguin nests each year between 2001 and 2010, excluding nests occupied by birds that were de-oiled following the *Treasure* oil-spill of 2000 as this cohort had poorer breeding success in some years than birds that never been oiled (Barham *et al.* 2007; Sherley 2010).

In all years, the monitoring visits covered the main breeding season at this locality (early March to late August; Crawford *et al.* 1995b) but in some seasons checks of nests were made as early as mid-February and as late as mid-November. Most nests were selected for monitoring during March and April but some nests were added to the sample throughout the breeding season in all years (Barham *et al.* 2007). Nests were normally checked at intervals of 4–7 days, but were sometimes checked at intervals of 14–28 days. The type of nest (see Table 1, Figs 1, 2) was recorded at the first visit and all nests were checked as part of a series of ‘nest-rounds’. Thus, any nests active at any given time were checked on one day or over two consecutive days and monitoring intensity did not differ between types of nests. The

**Table 1.** Types of nest and criteria used to classify African Penguin nests on Robben Island, 2001–2010

Nest type name	Code	Description
Open	O	Open scrape; not under any substrate; no shelter from sun, rain, etc.
Under vegetation	V	Scrape under vegetation (e.g. Rooikrans); some shelter
Building/Man-made	B	In disused buildings or under man-made materials; ~100% shelter
Artificial nest	A	Custom-made artificial burrow or nest-box; 100% shelter
Natural burrow	N	Natural burrow in sandy soil; 100% shelter; roof can collapse



**Fig. 2.** Examples of the four natural types of nest monitored for African Penguin breeding success and nest survival on Robben Island, 2001–2010. Birds bred in: (a) surface nests in the open; (b–c) surface nests under vegetation, principally Rooikrans; (d–e) disused and abandoned buildings or under other man-made structures; and (f) natural burrows dug in sandy substrate. See Table 1 for types of nest monitored in this study.

study nests were not always followed from before laying or continuously after the breeding attempt was complete, so it was not always possible to determine whether the breeding attempts monitored represented first, replacement or second clutches. Although most nests were first visited during incubation (~85%) some nests were first monitored after chicks had already hatched.

On each visit to a nest, the number of any eggs or chicks was noted. Chicks were not weighed but were classified into five stages of development, from P0 to P4 (following Barham *et al.* 2007), and considered to have fledged successfully if they reached the fifth stage (P4). Some chicks that were recorded as fledging at <60 days after hatching may have wandered from their nests and thereby evaded detection at subsequent checks. In addition, many chicks eventually joined crèches and, although neighbouring nests and crèches were checked for the presence of ‘missing’ chicks, they could not always be positively identified. Breeding success may, therefore, be overestimated.

#### *Nesting success*

To account for the bias induced by the monitoring protocol, an extension of the Mayfield (1961, 1975) method was used to determine nesting success. Nest-days were calculated by taking the mid-point between visits to nests (Mayfield 1961). If the hatching date could not be reliably estimated because of unusually long intervals between visits then the estimate of nest-days was constrained so as not to be greatly longer than the maximum interval between laying and hatching of 41 days (e.g. Rand 1960). Exact visit times were not recorded, so nest-days were calculated to the nearest half-day.

Parametric survival models, specified using the *survreg* function in R v2.10.1 (R Development Core Team 2009) were used to determine the daily failure rates and the probability of the nest-contents surviving through the incubation and chick-rearing periods (Sherley *et al.* 2011). An exponential error distribution was employed to estimate the survival distribution as this assumes that nests fail with a constant probability over time (Crawley

2007; Zador *et al.* 2009). Data were considered right censored (Venables and Ripley 1999: p. 365) if the nest persisted through the end of the study period and, thus, the time to death was not known. Following Sherley *et al.* (2011) the maximum likelihood estimate of risk of failure ( $F$ ) per sampling interval (approximately equivalent to the number of nest failures/total nest days) for nests with eggs and chicks was defined as:

$$F = \exp(-\alpha - \beta x) \quad (1)$$

where  $\alpha$  and  $\beta$  are the estimated parameters from the model (intercept and coefficients) and  $x$  is the value of the explanatory variable (fixed as  $x = 1$  for factorial variables). Nest survival ( $S$ ) at time  $t$  was, therefore, defined as:

$$S(t) = \exp(-Ft) \quad (2)$$

for a model with one explanatory variable. For the incubation period,  $t$  was assumed to be 40 days (e.g. Rand 1960) and for the fledging period  $t$  was taken to be 74 days (Wolfaardt *et al.* 2008). As daily mortality rates differ for different nesting stages (Seddon and van Heezik 1991) the incubation and chick-rearing periods were considered separately and the survival rates for the whole breeding attempt were determined from the product of the two. Approximate upper and lower 95% confidence intervals (CI) for nest survival are given by:

$$\exp(-t(F - 1.96 F/\sqrt{n})) \text{ and}$$

$$\exp(-t(F + 1.96 F/\sqrt{n}))$$

where  $n$  is the number of failed breeding attempts occurring during either incubation or chick-rearing.

As the sample sizes in the different types of nest varied between years, and because African Penguins show interannual variation in breeding success (e.g. Crawford *et al.* 2006), the year was included along with the type of nest as an explanatory variable in the survival models used to compare between the types of nest. However, in most cases, the sample sizes were too small to make meaningful within-year comparisons so, where effects are presented, the survival rates and confidence intervals are based on all 10 years of data.

#### Breeding productivity

As the nest-success models described above do not index partial failures (e.g. the loss of one egg or chick is ignored), we also compared incubation success using apparent clutch-size, the incidence of infertile eggs and hatching success (the proportion of chicks hatching from eggs laid). Eggs were considered infertile if they survived for >42 days but did not hatch (following Wolfaardt *et al.* 2008) and differences were tested using Fisher's Exact Test. Apparent clutch-size was compared using the proportion of one- and two-egg clutches at the first visit to a nest by scoring two-egg clutches as successes and one-egg clutches as failures (not accounting for mortality before the onset of monitoring).

Fledging success was determined using the proportion of chicks fledged from the number of chicks hatched and the proportion of breeding attempts fledging one and two chicks (scoring two-chick nests as successes and one-chick nests as failures). Generalised Linear Models (binomial error distribution,

logit link function) were used to analyse all proportional data (Crawley 2007), with the models specified in R v2.10.1 (R Development Core Team 2009). For breeding attempts that were first visited during incubation and where an outcome could be determined (i.e. eggs were monitored to hatching and chicks to fledging), we also calculated the number of chicks fledging per pair and per breeding attempt in each type of nest. As nests were not always followed from before laying, and because fledging could not always be confirmed with certainty (see above), these measures of breeding success will be biased. Thus, they are presented purely to enable comparison with previous studies (e.g. Crawford *et al.* 2006; Kemper *et al.* 2007a, 2007b) and were not compared statistically.

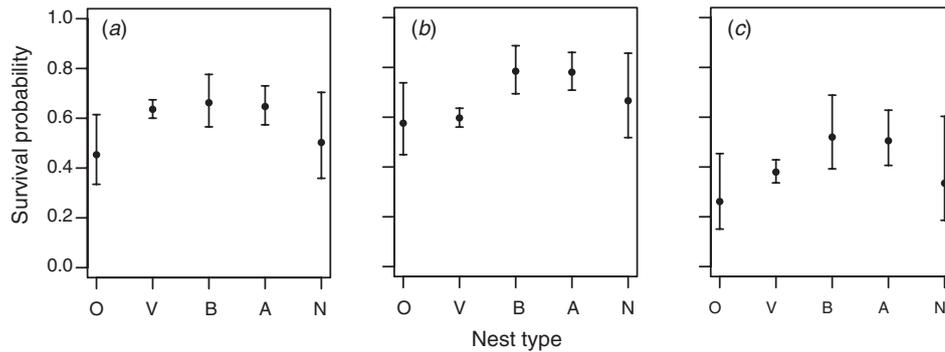
#### Results

An estimate of nest-days for the incubation period was available from 1186 breeding attempts whereas an estimate for the chick-rearing period could be obtained from 1013 breeding attempts where the type of nest had been recorded. In total, 1115 breeding attempts were followed from incubation until a conclusion was reached. Eggs hatched in 764 and chicks fledged in 438 of these attempts. Breeding productivity parameters are thus based on those attempts. For the years where breeding attempts were available from both the wooden boxes and the fibreglass burrows (2007–2010 inclusive), nesting success did not differ between the two during either the incubation period (boxes = 0.649, burrows = 0.690;  $z = 0.39$ ,  $P = 0.70$ ,  $n = 137$ ) or chick-rearing period (boxes = 0.727, burrows = 0.902;  $z = 1.51$ ,  $P = 0.13$ ,  $n = 91$ ). Hatching success (boxes = 86.5%, burrows = 86.5%;  $z = -0.003$ ,  $P = 0.99$ ,  $n = 84$ ) and fledging success (boxes = 61.5%, burrows = 68.9%;  $z = 0.749$ ,  $P = 0.45$ ,  $n = 84$ ) were also similar, so the boxes and burrows were combined as 'Artificial Nests' for further analysis. As vegetation nests were used by most breeding pairs on the island, the vegetation nest-type was set as the intercept for all models.

#### Nesting success

The models containing both the Year and Nest-type terms were preferred to the model containing Nest-type alone during both the incubation (Year + Nest-type AICc = 3784.8, Nest-type AICc = 3813.6) and chick-rearing periods (Year + Nest-type AICc = 3917.9, Nest-type AICc = 3937.6). With both terms retained in the model, the annual probability of a nest surviving incubation in the vegetation nest-type ranged from 0.313 (95% CI = 0.207–0.475) in 2001 to 0.753 (0.697–0.814) in 2008. With nests under vegetation set as the baseline for the model (0.636, 95% CI = 0.607–0.669), only nests in the open had a significantly poorer probability of survival during incubation (0.453, 95% CI = 0.335–0.615; coefficient estimate = -0.72,  $z = -3.16$ ,  $P = 0.002$ ; Fig. 3a).

During the chick-rearing period, nesting success was significantly better in nests in buildings (coefficient estimate = 0.80,  $z = 2.98$ ,  $P = 0.003$ ) and in artificial nests (coefficient estimate = 0.73,  $z = 3.45$ ,  $P < 0.001$ ) than in nests under vegetation (Fig. 3b), but the latter did not differ from natural burrows (coefficient estimate = 0.32,  $z = 0.98$ ,  $P = 0.33$ ) or nests located in the open (coefficient estimate = -0.17,  $z = -0.64$ ,  $P = 0.52$ ; Fig. 3b). The parametric survival model was not applied to the



**Fig. 3.** The probability of an African Penguin nest surviving for each of the five types of nest on Robben Island, 2001–10: (a) for the average incubation period of 40 days; (b) for the average chick-rearing period of 74 days; and (c) for the whole breeding attempt. The probability for the whole breeding attempt (c) is derived by multiplying the survival probabilities from the incubation and chick-rearing periods. These points are the probabilities from the 10 breeding seasons combined; the vertical lines are the 95% confidence limits of the survival probabilities. Nest-types: O, Open; V, Under vegetation; B, Building/Man-made; A, Artificial nest (including burrows); N, Natural burrow (see Table 1 for details).

data for the whole breeding attempt combined but, given that survival during the incubation period was almost identical in nests under vegetation, artificial nests and nests in buildings (Fig. 3a) and was greater in the latter two over the chick-rearing period (Fig. 3b), it is reasonable to conclude that the differences in the probabilities of nests surviving in artificial nests and nests in buildings (relative to nests under vegetation) over the whole breeding attempt (Fig. 3c) are meaningful.

### Breeding productivity

#### Apparent clutch-size and infertile eggs

The apparent mean clutch-size ( $\pm$ s.d.) in nests in buildings ( $1.85 \pm 0.36$ ), natural burrows ( $1.85 \pm 0.36$ ) and in artificial nests ( $1.85 \pm 0.36$ ) was similar to that of nests under vegetation ( $1.87 \pm 0.34$ ; all  $P > 0.05$ ), but was significantly lower in open nests ( $1.76 \pm 0.43$ ) compared to those under vegetation ( $z = -2.24$ ,  $n = 1115$ ,  $P = 0.025$ ). The apparent proportion of infertile eggs did not differ significantly between the five groups (Fisher's Exact Test,  $P = 0.53$ ; Table 2).

#### Hatching success

Hatching success (the proportion of eggs laid that survived the incubation period) was 12.8% higher in nests under vegetation than in natural burrows ( $z = -2.23$ ,  $P = 0.026$ ,  $n = 1115$ ) and 10.8% higher than in open nests ( $z = -2.08$ ,  $P = 0.038$ ). Hatching success for both the nests in buildings and the artificial nests were similar to nests under vegetation (Table 2; all  $P > 0.05$ ). In breeding attempts where at least one egg survived the incubation period ( $n = 764$ ), none of the nest-types differed significantly from nests under vegetation in terms of the proportion of hatchlings per egg laid (Fig. 4a; all  $P > 0.05$ ).

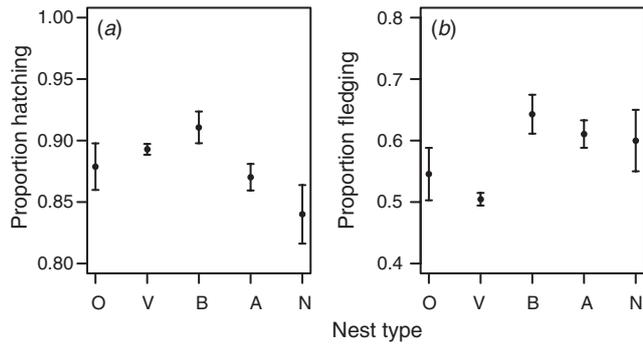
#### Fledging success

Both nests in buildings ( $z = 2.49$ ,  $P = 0.014$ ,  $n = 764$ ) and artificial nests ( $z = 2.22$ ,  $P = 0.026$ ) fledged significantly more chicks per egg that hatched than the nests under vegetation, whereas the natural burrows and open nests did not differ significantly from the baseline (fledging success in Table 2, Fig. 4b). The proportion of breeding attempts fledging two chicks ranged from 0.53 in the artificial nests to 0.68 in the nests in the

**Table 2.** Summary of breeding success parameters for African Penguins in the five different types of nest on Robben Island, 2001–2010

Hatching success is per egg laid and fledging success per egg hatched. Success rate shows the percentage of breeding attempts fledging at least one chick. MCF, mean number of chicks fledged ( $\pm$ s.d.). See Table 1 for explanations of the nest types

Breeding success parameter	Open (O)	Vegetation (V)	Building (B)	Artificial (A)	Burrow (N)	Total
Number of pairs	54	713	78	136	40	1021
Number of breeding attempts	59	779	82	154	41	1115
Number of eggs laid	104	1456	152	285	76	2073
Proportion infertile	0.09	0.12	0.14	0.13	0.16	0.14
Number of eggs hatched	56	933	95	175	39	1298
Hatching success (%)	53.8	64.1	62.5	61.4	51.3	62.6
Number of chicks fledged	32	485	62	107	23	709
Fledging success (%)	57.1	52.0	65.3	61.1	58.9	54.6
Success rate (%)	32.2	38.1	45.1	45.5	38.5	39.3
MCF per breeding attempt	$0.54 \pm 0.84$	$0.62 \pm 0.85$	$0.76 \pm 0.90$	$0.70 \pm 0.83$	$0.56 \pm 0.81$	$0.64 \pm 0.85$
MCF per pair	$0.60 \pm 0.86$	$0.68 \pm 0.89$	$0.79 \pm 0.97$	$0.79 \pm 0.89$	$0.58 \pm 0.87$	$0.70 \pm 0.89$



**Fig. 4.** Two measures of breeding success from breeding attempts undertaken by African Penguins nesting in five different types of nest on Robben Island, 2001–2010: (a) the mean proportion of eggs hatching (per egg laid) in breeding attempts that survived incubation in the five types of nest; and (b) the mean proportion of chicks fledged per egg that hatched in the five types of nest. The vertical lines show the standard error of the mean. Nest-types: O, Open; V, Under vegetation; B, Building/Man-made; A, Artificial nest; N, Natural burrow (see Table 1 for details).

open, but the sample sizes were small for all but the vegetation nest-type and the differences were not significant (all  $P > 0.05$ ,  $n = 438$ ).

Over the 10 years of the study, both the nests in buildings and artificial nests fledged 11% more chicks per pair and fledged 14 and 8% more chicks per breeding attempt than the nests under vegetation (Table 2). However, these estimates are likely to be confounded (see Methods), so the differences were not tested statistically.

## Discussion

Nesting in holes is basic to the biology of *Spheniscus* penguins (e.g. Frost *et al.* 1976a; Boersma 1977) and, before the depletion of the deposits in southern Africa, African Penguins nested preferentially in burrows dug into guano or other soft substrates throughout much of their range (e.g. Frost *et al.* 1976a; La Cock 1988). Burrows confer a thermoregulatory advantage on breeding birds by protecting them against diurnal temperature fluctuations (Frost *et al.* 1976a) and are known to reduce chick mortality in some cases (Frost *et al.* 1976b; Cooper 1980; cf. Seddon and van Heezik 1991). They are, however, scarce at most breeding colonies of African Penguins because of the large scale removal of guano and birds now generally nest in caves (Bartlett *et al.* 2003), rock crevices (Frost *et al.* 1976b), non-guano burrows or on the surface (e.g. La Cock 1988).

The penguin colony on Robben Island was extirpated at some point in the late 1790s (Crawford *et al.* 1995b) and only re-colonised in 1983 (Shelton *et al.* 1984). By this time stands of introduced vegetation had come to dominate the island flora (Brooke and Prins 1986). As a result, most African Penguin nests on Robben Island are shallow surface scrapes, under introduced shrubs (Crawford *et al.* 1995b). Burrows are scarce on Robben Island, accounting for only 1.2% of nests in 1992 (Crawford *et al.* 1995b) for example, and the sandy soils that dominate the interior of the island make burrows prone to collapse (R. B. Sherley, pers. obs.). Robben Island has at times supported a population in excess

of 7000 pairs of Penguins (see Table 1 in Underhill *et al.* 2006), birds have bred successfully since 1983 (e.g. Crawford *et al.* 1999; 2006) and the reproductive output in this study (0.7 chicks per pair) was on par with or surpassed that previously recorded at other breeding colonies (see Table 6 in Kemper *et al.* 2007b). This suggests that nests under vegetation may be, at the very least, adequate breeding habitat. At Boulders Beach, where many pairs also breed under introduced vegetation, Hampton *et al.* (2009) found that nesting success in nests under vegetation did not differ significantly from that in natural burrows, albeit in only one breeding season.

In this study, although the nests in natural burrows did not differ significantly from the nests under vegetation in the survival models, natural burrows had the lowest hatching success of any nest-type and this was significantly lower than in nests under vegetation. This may indicate a higher incidence of partial failure than the other types of nests, as the survival model does not account for partial failures. However, as collapses (La Cock 1988; Seddon and van Heezik 1991) and flooding in heavy rain (Wilson and Wilson 1989; Seddon and van Heezik 1991) are likely to be the main causes of egg and chick mortality in natural burrows (e.g. Wilson and Wilson 1989; Seddon and van Heezik 1991), it is difficult to see why partial failures during incubation should have been more common than in nests under vegetation, but not total failures. It is possible that the inability to detect a difference with the survival model resulted from the small sample size of natural burrows giving rise to a Type II error. Klett and Johnson (1982) recommended a minimum of 50 nests for comparisons using the Mayfield method approach and survival analyses also require fairly large sample sizes to detect significant differences (Crawley 2007; Kemper *et al.* 2007a). The wide confidence intervals associated with the survival probabilities for the natural burrows indicate a lack of accuracy in estimating the survival rates.

For birds breeding in the open, the higher incidence of complete failure during incubation was most likely the result of birds abandoning nests owing to exposure to environmental factors, such as heat stress (e.g. Crawford *et al.* 1995b), although predation could also have been a factor. Kelp Gulls (*Larus dominicanus*) take abandoned Penguin eggs on Robben Island (R. B. Sherley, pers. obs.) and at some colonies Gulls sometimes harass surface nesting Penguins, forcing them to temporarily expose the nest-contents, which are then eaten (Kemper *et al.* 2007b). Mole Snakes (*Pseudaspis cana*) and Feral Cats (*Felis catus*) also occur on Robben Island and take abandoned Penguin eggs (Crawford *et al.* 1995b; Dyer 1996) but it is possible that both could also harass incubating birds on exposed nests. A Mole Snake has been recorded attempting to raid an active Penguin nest (under vegetation) on one occasion (Underhill *et al.* 2009). Active harassment of incubating Penguins by predators has not been recorded on Robben Island but it could occur and have gone unnoticed because of the scarcity of open surface nests.

For birds nesting in the open, human disturbance may also cause temporary abandonment, leading to predation or failure of eggs. Birds nesting under some kind of cover are less likely to flee their nests during disturbance by people (Kemper *et al.* 2007a; R. B. Sherley, pers. obs.) and passage disturbance through low-density colonies can result in loss of eggs to Kelp Gulls (Hockey and Hallinan 1981). The Penguin colony on Robben Island is theoretically off-limits to tourists visiting the island, but occa-

sionally curious members of the public are found wandering in the main Penguin breeding areas. These infrequent occurrences, along with disturbances caused during monitoring work, may lead to increased abandonment of open nests.

Over the 10 years, birds breeding in artificial nests and buildings fledged 8 and 14% more chicks per breeding attempt than birds nesting under vegetation. The elevated success in these nests was attributable to a higher probability of survival during the chick-rearing period. On Halifax Island, nest survival in buildings was inferior to that of all other types of nests during chick-rearing (Kemper *et al.* 2007a). The poorer success on Halifax was attributed to near-permanent damp conditions and resultant high presence of exoparasites (Kemper *et al.* 2007a). On Robben Island, most of the buildings are not continuously damp (R. B. Sherley, pers. obs.) and this may explain the difference between the two studies. Survival of chicks was superior in artificial nests compared with surface nests and nests under shrubs during the chick-guard stage (the first 42 days of the chick-rearing stage) on Halifax Island, but similar in the post-guarding stage (the remaining days of the chick-rearing stage; Kemper *et al.* 2007a). During the first half of the guard stage (~20 days), chicks have not yet reached thermal independence (Erasmus and Smith 1974) and are largely immobile (Seddon and van Heezik 1993). They are therefore still susceptible to mortality from environmental effects, such as flooding. In the later stages, when left unguarded by their parents (Seddon and van Heezik 1993), chicks in surface nests, compared with those from artificial nests and buildings, may wander more in search of shelter (Wilson and Wilson 1989) or more readily flee in response to human disturbance (Kemper *et al.* 2007a). This may make them more susceptible to suffering aggressive interactions with other breeding adults or put them at greater risk of predation (Cooper 1977). Feral Cats on Robben Island can take chicks at least up to the P3 stage (Crawford *et al.* 1995a) and when chicks must be left unguarded so that both adults may forage to meet the increasing energetic requirements of the chicks (Cooper 1977), chicks in open nests and nests under vegetation may be more susceptible to predation than those in buildings or artificial nests. However, we did not have information on the age-structure of the birds occupying the various types of nests because the population on Robben Island is largely not individually marked (predominately as a result of concerns about flipper banding, see e.g. Petersen *et al.* 2005). We were therefore not able to separate the direct effect of quality of nest-type and parental quality (e.g. chick-rearing efficiency linked to breeding experience; e.g. Weimerskirch 1990) and it is possible that better quality or more experienced pairs are more likely to occupy and retain sheltered nesting sites.

Artificial nests and buildings on Robben Island may offer the benefits of burrows to breeding Penguins, such as protection from heat stress and predation, without the disadvantages of collapse or flooding. However, several studies of artificial nests provided to secondary hole-nesting birds have indicated that nest-characteristics can interact with the local physical and biotic environment to influence success (see Lambrechts *et al.* 2012 for a review). The same is likely to be true for penguins, with the success of any artificial nests being design dependent and site-specific. Ropert-Coudert *et al.* (2004) found that temperatures in nest-boxes used by Little Penguins (*Eudyptula minor*) in Western Australia were consistently higher than in surround shrubs, postulating poor

ventilation as the cause, whereas Griffin (2005) suggested that temperatures showed greater variability in the artificial nests on Robben Island than in vegetation nests for the same reason. The artificial burrows developed in South Africa are designed to mimic the optimal habitat of natural burrows, but determining whether they achieve this goal will require additional studies addressing the relative differences between the wooden boxes and the artificial burrows over a long time-frame. Studies to assess the efficacy of the artificial burrows in increasing breeding success in the long term are ongoing and attempts are being made to optimise several aspects of their design, placement and installation following feedback from field studies such as this one and those taking place at other colonies (Pichegru, *in press*; L. J. Waller, pers. comm.). Studies of rates of chick-growth and condition of chicks should also be instigated to assess whether birds occupying artificial nests also produce chicks of higher quality that grow faster and fledge in better condition than their counterparts in vegetation or open nests.

Besides improving breeding success, sheltered nesting sites may also be involved in attracting new recruits to breeding colonies. Crawford *et al.* (1995b) have suggested that the availability of nesting space under shade may have been one of the factors leading to Robben Island being re-colonised by first-time breeders in 1983. We were not able to determine whether the artificial nests used in this study were being occupied by birds that had previously bred in sites under vegetation on Robben Island or first-time breeders moving in to occupy them (see above regarding individual markers). African Penguins display a degree of nest-site fidelity but they will move nesting sites, particularly following an unsuccessful breeding attempt (La Cock and Cooper 1988). They also show strong fidelity to breeding colonies once they have bred successfully (Whittington *et al.* 2005). Artificial nests could, therefore, be useful both in attracting birds away from poor breeding sites (e.g. nests in the open) and in encouraging and retaining first-time breeders at colonies with poor population trajectories (e.g. Dyer Island; Crawford *et al.* 2011) or where breeding has previously ceased (e.g. Bird Island, Lambert's Bay; Crawford *et al.* 2011). However, whether artificial nests could be used in this way still remains to be investigated and availability of food probably also plays a vital role in determining to where first-time breeders recruit (Crawford *et al.* 2001). Subsequently, any efforts to improve breeding habitat using artificial nests must be concurrent with efforts to protect the prey base of African Penguins (e.g. Durant *et al.* 2010).

Nest-boxes have been used to improve the breeding success of Little Penguins in New Zealand and Australia (e.g. Perriman and Steen 2000) and artificial nests have been trialled for Humboldt Penguins (*Spheniscus humboldti*) in Peru and Chile (Paredes and Zavalaga 2001; Simeone *et al.* 2010). They have not, however, been used for other *Spheniscus* penguins to the extent that they are currently in use in South Africa. Although questions remain, our study suggests that the provision of artificial nests can improve breeding productivity for penguins nesting in temperate climates and could help to stem the decline of the African Penguin both on Robben Island and further afield.

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