

## RESEARCH ARTICLE

## Decades of artificial nests towards African penguin conservation—Have they made a difference?

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## Abstract

1. African penguins are among the most threatened seabird species globally and an African Penguin Biodiversity Management Plan (BMP) published in 2013 guides conservation strategies to prevent their extinction. To counter the impact of past guano exploitation which reduced the nesting habitat of these burrowing seabirds, rendering them vulnerable to predators and extreme weather events, a suite of artificial nests was deployed in various colonies over the past decades with varying success. The BMP called for new nest designs to maximise breeding output.
2. This study assesses African penguin breeding success over the past 14 years in four types of artificial nests and in natural nests at all major colonies in South Africa.
3. Overall, artificial nests outperformed natural nests and successfully increased breeding output of African penguins by 16.5% (95% CI: 6.7–26.2). No design was, however, consistently most effective across locations. For example, fibre-glass nests had the poorest hatching success of all nest types at one colony (Bird Island), but outperformed cement nests at another (Boulders Beach). The latest design of double-layered ceramic nests tended to perform better than other artificial nests, although not consistently at all colonies and occupancy rates were low in some areas.

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4. *Practical implication.* The deployment of artificial nests proved to be a successful conservation measure for African penguins although the variety of habitats in the different colonies seems to have prevented a one solution-fits-all approach. The consistent poor breeding output in some areas in all nest types (<30% at the mainland colony in Simons' Town and the islands in Algoa Bay) further calls for colony-specific conservation strategies beyond artificial nests, while the continuous decline in African penguin numbers globally calls for broader measures urgently, primarily increasing access to their forage fish prey.

#### KEYWORDS

Biodiversity Management Plan, breeding success, climate change, conservation action, endangered species, Mayfield method, predation

## 1 | INTRODUCTION

Bird populations are usually limited by some combination of food availability and adequate nesting space (Newton, 1998). As species that feed at sea and breed on land, seabirds can be particularly vulnerable in the face of concurrent marine and terrestrial threats (Dias et al., 2019). For those that breed in regions with permanent human settlements, factors like habitat degradation at breeding colonies can be important contributors to population decline (Dias et al., 2019; Ropert-Coudert et al., 2019) and artificial structures, such as artificial nests, have been provided in attempts to improve the conservation status of cavity nesting seabird species (e.g. Bourgeois et al., 2015; Libois et al., 2012; Sutherland et al., 2014).

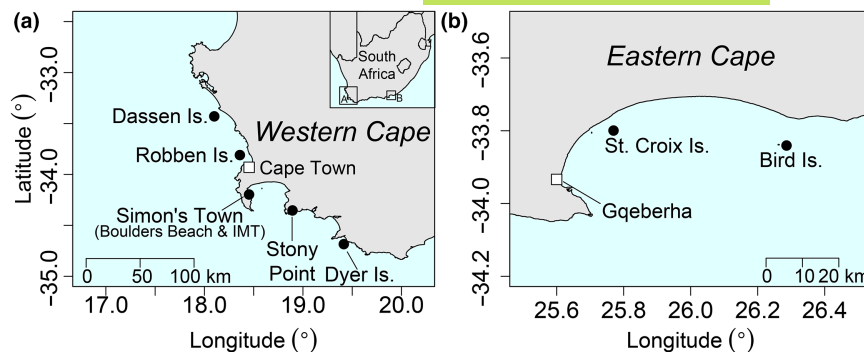
The African penguin *Spheniscus demersus* is endemic to Southern Africa and currently faces an extremely high risk of becoming extinct in the wild (Sherley et al., 2024). Notwithstanding a brief recovery in the late 1990s and early 2000s, their population has declined by ~90% during the last 70 years, from ~93,000 pairs in 1956 to ~9900 breeding pairs in 2023 (Crawford et al., 2011; Sherley et al., 2020, 2024). While the main cause of their recent decline is poor adult survival underpinned by a reduced availability of food (Crawford et al., 2011, 2019; Robinson et al., 2015), past guano exploitation in the 19th and 20th century reduced suitable breeding habitat for the African penguin, which continues to impact their breeding output to this day. African penguins naturally breed in burrows dug in guano—an adaptation to hot terrestrial habitats, as their morphological and physiological adaptations to cold water render them vulnerable to heat stress (Bertelli & Giannini, 2005). When faced with high air temperatures, adults can desert their nests to cool down in the sea (Frost et al., 1976), leaving the broods of surface nesters exposed to overheating and vulnerable to predators (particularly large Larids) (Yorio & Boersma, 1994). Natural burrows also shelter the broods from severe rains and wind, which can be fatal to the chicks (Frere et al., 1992; Randall et al., 1986; Seddon & van Heezik, 1991). Current climate change is rapidly increasing the frequency and duration of extreme weather events (Stott, 2016; van Wilgen et al., 2016), exacerbating the impact of habitat degradation on the penguin population. While little can

be done to tackle climate change in the short term, breeding habitat can be improved with proactive management (Ropert-Coudert et al., 2019) at the appropriate scale (Trathan et al., 2015). While the pressure for high quality nesting habitat has inevitably reduced in recent years due to the significant reduction in the numbers of breeding pairs, available nesting habitat remains short of optimal at certain colonies where there is little available shade or vegetation, and where there is no guano into which the penguins can burrow.

Habitat degradation has been identified as a key threat to African penguins since the 1990s, and habitat management has been considered one of the highest priorities for African penguin conservation in various workshops and management plans over time (BirdLife International, 2022; du Toit et al., 2002; Ellis et al., 1998). Strategies suggested included the provision of 'drainage and shade' (Ellis et al., 1998), the 'provision and maintenance of aesthetically pleasing artificial burrows' or the provision of 'artificial nesting sites to compensate for the threats posed by guano scraping, extreme weather conditions or loss of breeding sites, as well as to limit the impact of mammal-bird competition' (Du Toit et al., 2003).

Artificial nests or burrows have thus been placed in various African penguin colonies in South Africa and Namibia for over 30 years (see Wilson & Wilson, 1989) in an attempt to increase breeding habitat availability or improve breeding output, with varying success (Lei et al., 2014; Sherley et al., 2012). Wooden boxes deployed on Robben Island (Figure 1) in 2001 successfully increased fledging success compared to nests under vegetation (Sherley et al., 2012). Later, fibreglass nests (see Methods) were deployed at several major African penguin colonies and studies revealed contrasting performance at different locations. Their breeding success was higher to that of vegetation nests on Robben Island (Sherley et al., 2012; Tol, 2016), similar at Stony Point (Hugo, 2021) but lower on Bird Island (Pichegru, 2013) and Dyer Island (Hugo, 2021). Due to these divergent results, the African Penguin Biodiversity Management Plan (BMP) published in 2013 called for a 'Working Group [that] must oversee the research of artificial nests suitability and if deemed appropriate,

**FIGURE 1** Location of African penguin colonies monitored for breeding success between 2008 and 2022, in (a) the Western Cape and (b) the Eastern Cape of South Africa.



to develop guidelines for their manufacture, deployment and assessment' (Action 2.1.2) (Department of Environmental Affairs [DEA], 2013). A new type of artificial nest for African penguins, that is, double-layered ceramic nests (see Section 2 for details), was therefore designed, tested on land for physical conditions in the nests (Malan & Graham, 2020) and deployed in various colonies from 2018 onwards. They were monitored concomitantly in all colonies thereafter.

This study reports on the monitoring of breeding success in these new nests as well as three other types of artificial nests over a 14-year period and across eight colonies of African penguins in South Africa to compare their success with that of various natural nests. Here, we begin to examine the contrasting success of various nest artificial nest types at different colonies and undertake the first consolidated assessment of the overall impact of artificial nests, a nation-wide conservation measure, on African penguins in South Africa.

## 2 | METHODS

### 2.1 | Breeding success monitoring

All research was conducted under permits approved by the Department of Forestry, Fisheries and the Environment, SANParks and/or CapeNature. Methods were approved by the Ethics Review Bodies at the University of Bristol, the University of Cape Town, the University of Exeter and Nelson Mandela University at different times during the lifetime of the project.

African penguins typically lay a clutch of two eggs (Hockey et al., 2005). Most nests were selected during incubation, although some were monitored continuously each year, and others selected at a later stage. In most colonies, nests were selected randomly in various areas of the colony, but at Robben Island, all nests in a selected area were monitored, with nests being added when eggs were laid throughout the season. The nests' contents (number of adults, eggs, chicks and size of chicks) were monitored every 7–10 days. If the eggs disappeared between successive checks, the nest was assumed to have failed at the incubation stage. After 6–8 weeks, the chicks may leave their nests to join crèches (Seddon & van Heezik, 1993) and are not reliably associated with individual nests. Hence, we

assumed that a nest was successful (up to the post-guard stage) if the chicks were known to have reached 8 weeks of age and the nest bowl was unoccupied. Reason for mortality could generally not be determined and, even when this was possible, it was not systematically noted across years and colonies. It was, therefore, not included in this study. Each breeding attempt in a marked nest was considered independently, as most birds were not individually marked, and more than one pair may occupy a nest site in a season in some colonies (Barham, 2017). While nest desertion due to disturbance by researchers was not systematically noted, African penguins breeding in the monitored areas used in this study are generally habituated to the presence of researchers (Scheun et al., 2021) and only very rarely desert their nests temporarily after human disturbance (Pichegru et al., 2016).

### 2.2 | Study site description

African penguin breeding success was monitored across eight colonies in South Africa between 2008 and 2022 (Figure 1). Dassen Island (32°25' S, 18°05' E) is a large (220 ha), predominantly sandy and flat island, with the majority of penguins nesting in burrows excavated in sand, or between boulders and under shrubs (Wolfaardt, 2000). Robben Island (33°48' S, 18°22' E) is the largest of the islands off the coast of South Africa, with an area of 507 ha, and is covered by exotic vegetation such as rooikrans *Acacia Cyclops*, manatoka *Myoporum serratum* and various *Eucalyptus* that penguins use as nest sites (Tol, 2016). The mainland colony of Boulders Beach (34°11' S, 18°26' E) is not only located in the urban area of Simon's Town, with birds breeding on the beach and under vegetation in a National Park and an area under the management of the City of Cape Town but also extends across a busy road as well as in private residential gardens. Stony Point (34°22' S, 18°53' E) is also a mainland colony, located in a vegetated area around a rocky point and consisted of two municipal properties about 8.39 ha in size (Hugo, 2021). Dyer Island (34°24' S, 19°15' E) is a flat island, 20 ha in size ca. 6 m above sea level, with mixed vegetation over a pebble-covered surface. St Croix (33°48' S, 25°46' E) is a 12 ha rocky, steep island rising 58 m above sea level, with sparse vegetation. Finally, Bird Island (33°50' S, 26°17' E) is relatively flat, 19 ha in size about 9 m above sea level, covered with sparse vegetation that provides little cover for penguins.



## 2.3 | Artificial nests description

Wooden A-framed boxes (Figure 2a) are free-standing structures constructed from 3-mm thick pine plywood, varnished on the outer surface. The boxes are constructed to form a triangular prism (790 (l) × 430 (h) mm on each side and 380 (h) × 380 (w) mm at the back of the box). The front of the box is reinforced with a piece of wood 380 mm long (across the base of the entrance), but otherwise left open (Figure 2a). An opening (c. 70 (h) × 90 (w) mm) is left near the top of the back of the box for ventilation. These wooden boxes were deployed on Robben Island in 2001, to compensate for the removal of alien vegetation used by penguins for breeding (Sherley et al., 2012). They have been monitored since 2001 and are part of the longest existing monitoring programme on African penguins.

Cement nests made of a mixture of fibreglass and cement, approximately 30 cm high and 50 cm deep (Figure 2b) were deployed

at Dyer Island, Boulders and Stony Point between 2003 and 2005. Different types of cement nest, made of cement pipes cut longitudinally in half ca. 30 cm high, 70 cm long and 10 mm thick and opened on both ends (Figure 2c), were deployed on Bird Island in 2011, although no numbers were tracked. Most of them are now covered with vegetation and difficult to monitor (L. Pichegru, pers. obs.).

Fibreglass burrows were manufactured from fibreglass mesh and resin by the Dyer Island Conservation Trust (DICT, <http://www.dict.org.za/>) from 2005 onwards and aimed at mimicking the shape of a natural African penguin burrow. They are 60 cm long, 40 cm wide and 30 cm high, with an opening 25 cm wide and 28 cm high (Figure 2d). Most were covered with rocks or soil upon deployment from 2006 until 2016, and some were overgrown with vegetation within 1 or 2 years. However, a number of fibreglass nests remained exposed with no coverage, while some filled up with sand and became unusable.



**FIGURE 2** Artificial nests for African penguins: (a) wooden A-framed box from Robben Island (extracted from Sherley et al., 2012); (b) cement nest as deployed at Boulders Beach, Stony Point and Dyer Island (© M. Ruthenberg) and (c) on Bird Island (© B. Diley); (d) fibreglass burrows prior to deployment (extracted from Sherley et al., 2012); (e) double-layered ceramic nest (© K. Graham); (f) open surface nests (© C. Lawrence); (g) vegetation nest (© K. Ludynia); and (h) natural burrows (© L. Upfold).

Ceramic nests (Figure 2e) are the latest design of artificial nests for African penguins, hand-manufactured by applying several layers of slurry-soaked geotextile over a mould. The slurry is a concoction of a ceramic powder, water and a waterproofing agent. They have been manufactured by DICT since 2016 and installed at most colonies from 2018 onwards. They are double layered with a 5-cm air gap and have a roof slanted at 27°. The height at the entrance is 20 cm and the height at the highest point is 50 cm, with an overall length of 60 cm and a width of 40 cm. The back side is closed except for seven holes for ventilation.

Various natural nest types were monitored at different colonies: surface open nests (Figure 2f), nests under vegetation (Figure 2g) and natural burrows (Figure 2g).

Types of nests monitored at the various colonies across the different years is shown in Table 1.

## 2.4 | Analysis of breeding data: The Mayfield method

To account for biases induced by the monitoring protocol (e.g. it being unclear in some cases if chicks fledged or disappeared), an extension of the Mayfield (1961, 1975) method was used to determine nesting success. For each egg and each chick, we calculated the number of days exposed to potential mortality (egg days or chick days) by taking the midpoints between visits to nests (Mayfield, 1961) and recorded whether mortality occurred (=1) or not (=0). Exact visit times were not recorded, so nest-days were calculated to the nearest half-day. In cases where the hatching date could not be reliably estimated because of unusually long intervals between visits, or birds appeared to incubate long-dead eggs for many days, the estimate of nest days was constrained to be 40 days (the maximum interval between laying and hatching is 41 days, e.g. Rand, 1960). We considered chicks to have died if they disappeared after <40 nestling days and no fate was clearly recorded (even if no carcass was observed). If chicks disappeared after ≥40 days, but had not been recorded in fledging plumage, we considered the monitoring to have been truncated (the observation was considered right censored) at the last time the chick was seen (Sherley et al., 2013). Accordingly, for censored observations, the time to death was imputed by the model using the interval distribution in JAGS (Plummer, 2003) as a random value greater than a specified censoring limit (Kruschke, 2015) based on the assumption that the individual egg or chick survived for at least one more day after they were last observed in the nest (Sherley et al., 2018, 2021).

## 2.5 | Statistical analyses

Previously we have used chick days data (as described above) to estimate chick failure rates (deaths/unit time of exposure or hazard functions) using an exponential hazard function and used an

exponential distribution to transform these failure rates into survival estimates (Sherley et al., 2013, 2015, 2018, 2021) as this is the simplest model structure (it assumes hazards [mortality rates] are constant over time). However, more recent work has shown that the mortality curve for African penguin chick survival is better described by a lognormal hazard function (Sydeman et al., 2021). Thus, here we undertook preliminary analysis using the *flexsurvreg* function from the 'flexsurv' library in R (Jackson, 2016) that used a frequentist approach with null models and no frailty terms to compare (graphically and statistically) exponential, Weibull, Gompertz, logistic, extreme and lognormal hazard functions. These preliminarily analyses supported using Weibull hazard functions to describe egg mortality and lognormal hazard functions to describe chick mortality.

Thus, here we estimated mortality rates (deaths/unit time of exposure) for different nest types using accelerated failure time models with a Weibull error distribution (implemented via the generalised Gamma distribution in JAGS) for eggs and a lognormal error distribution for chicks (Alvares et al., 2021; Christensen et al., 2010). We used year, colony and nest identity to specify hierarchical shared frailty terms, which are analogous to random effects (Therneau et al., 2003); that is, the survival rates of chicks within the same nest, colony and year could be considered non-independent. For egg survival, the mean hazard ( $\lambda$ ) was estimated as:

$$t_{i,j,k,l} \sim \text{GenGamma}(1, \lambda_{i,j,k,l}, \kappa),$$

$$\log(\lambda_{i,j,k,l}) = \beta x_k + \omega_j + \omega_{ji} + \omega_{j,i,k},$$

$$i = 1, \dots, I, \quad j = 1, \dots, Y, \quad k = 1, \dots, m_{ij} = M, \quad l = 1, \dots, n_{j,i,k} = N,$$

$$\omega_j \sim \text{Normal}(\alpha, \sigma_1^2), \quad \omega_{ji} \sim \text{Normal}(\omega_j, \sigma_2^2), \quad \omega_{j,i,k} \sim \text{Normal}(\omega_{ji}, \sigma_3^2). \quad (1)$$

where  $t_{i,j,k,l}$  denotes the observed time of exposure for each egg ( $l$ ), in nest  $k$ , in year  $j$ , at colony  $i$ ;  $\omega_j$  denotes a year shared frailty term;  $\omega_{ji}$  is a colony shared frailty term (nested in  $\omega_j$ );  $\omega_{j,i,k}$  a nest ID shared frailty term (nested in  $\omega_{ji}$ );  $\alpha$  is the random intercept;  $\beta$  is the nest type coefficient to be estimated;  $x_k$  is a covariate denoting the nest type; and the variances ( $\sigma$ ) of the shared frailty terms and the shape parameter ( $\kappa$ ) for the generalised gamma distribution were estimated from the data. For chick survival, the equivalent model was:

$$t_{i,j,k,l} \sim \text{Lognormal}(\Lambda_{i,j,k,l}, \tau),$$

$$\Lambda_{i,j,k,l} = \beta x_k + \omega_j + \omega_{ji} + \omega_{j,i,k},$$

$$i = 1, \dots, I, \quad j = 1, \dots, Y, \quad k = 1, \dots, m_{ij} = M, \quad l = 1, \dots, c_{j,i,k} = C, \quad (2)$$

$$\omega_j \sim \text{Normal}(\alpha, \sigma_1^2), \quad \omega_{ji} \sim \text{Normal}(\omega_j, \sigma_2^2), \quad \omega_{j,i,k} \sim \text{Normal}(\omega_{ji}, \sigma_3^2).$$

where  $t_{i,j,k,l}$  denotes the observed time of exposure for each chick ( $l$ ), in nest  $k$ , in year  $j$ , at colony  $i$ ;  $\omega_j$  denotes a year shared frailty term;  $\omega_{ji}$  a colony shared frailty term (nested in  $\omega_j$ );  $\omega_{j,i,k}$  a nest ID shared frailty term (nested in  $\omega_{ji}$ );  $\alpha$  is the random intercept;  $\beta$  is the nest type coefficient to be estimated;  $x_k$  is a covariate

**TABLE 1** Types of African Penguin nests included in this study that were monitored at each colony between 2008 and 2022. Details of sample size used in the statistical analyses are included in [Tables A1–A3](#).

	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022
<b>Wooden box</b>															
Robben Island	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<b>Cement</b>															
Bird Island				x	x								x	x	x
Boulders Beach													x	x	x
Dyer Island	x	x	x	x	x	x				x	x	x		x	x
Stony Point						x	x	x	x	x	x	x	x	x	x
<b>Ceramic</b>															
Bird Island													x	x	x
Boulders Beach													x	x	x
Dyer Island										x	x	x		x	x
Stony Point												x	x	x	x
<b>Fibreglass</b>															
Bird Island		x	x	x	x	x	x								
Boulders Beach													x	x	x
Dyer Island	x	x	x	x	x	x			x	x	x	x		x	x
Stony Point						x	x	x	x	x	x	x	x	x	x
<b>Vegetation/natural nests</b>															
Bird Island		x	x	x	x									x	
Boulders Beach															
Dyer Island	x	x	x		x					x					
Stony Point						x	x	x	x	x	x	x	x	x	x
Robben Island	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
St Croix Island	x	x	x	x	x	x									
Dassen Island	x	x	x	x	x	x	x	x	x	x	x	x			



denoting the nest type; and the variances ( $\sigma$ ) of the shared frailty terms and standard deviation ( $\tau$ ) for the lognormal distribution were estimated from the data. The total number of eggs ( $N$ ), chicks ( $C$ ), nests ( $M$ ), years ( $Y$ ) and colonies ( $I$ ) differed in each model and are specified in [Tables A1–A3](#) in [Appendix S1](#).

Models to estimate the effect of nest type on egg and chick survival were implemented using Markov chain Monte Carlo (MCMC) estimation in JAGS via the 'jagsUI' library (v. 1.5.2, Kellner, 2017) for program R (v. 4.3.0, R Development Core Team). The vague priors were Normal(0,  $10^{-6}$ ) for the  $\alpha$  and  $\beta$  parameters (where  $10^{-6}$  is precision), half-Cauchy(25) for the variance terms associated with the  $\omega$  (the frailty terms), Exponential(0.01) for the shape parameter ( $\kappa$ ) for the generalised gamma distribution and Gamma(0.001, 0.001) for the standard deviation ( $\tau$ ) of the lognormal distribution. We ran three MCMC chains of 500,000 samples, discarding the first 250,000 as burn-in, and thinned the chain to every 10th iteration. All models unambiguously converged ( $\hat{R}$  values  $\leq 1.01$ , smallest effective sample size  $> 300$ ). Unless otherwise stated, we present posterior means and 95% highest density intervals as credible intervals (95% CI) for egg survival at 40 days post laying, chick survival at 74 days post-hatching and for overall breeding success (the product of eggs and chick survival) at 114 days post-laying (Sherley et al., 2012, 2018, 2021). Effects are considered credibly different from zero if  $> 95\%$  of the posterior distribution had the same sign as the mean (i.e. the 95% CI did not overlap zero).

Finally, the number of monitored nests of each nest type sampled in each year since 2008 has varied greatly across the colonies at which artificial nests (of various kinds) have been placed (Sample size of each nest type monitored at each colony is given for each year in [Tables A1–A3](#)). It was not possible, therefore, to directly compare all nest types across all years and all colonies in one model. We thus adopted a stepwise analysis approach. First, we compared nests for all years (2008–2022) at all colonies in two broad nest types—artificial nests (any kind of man-made structure, including all types of custom designed artificial nest box or burrow) versus natural nests (including all nests in the open, nests under vegetation, nests under rocks and natural burrows) ([Table A1](#)). Second, we compared egg and chick survival in the four nest types that had been monitored at each of four colonies—Bird Island, Boulders Beach, Dyer Island and Stony Point—in at least 1 year between 2008 and 2022, namely Cement, Ceramic, Fibreglass and Vegetation nests (the latter included some open surface nests but excluded nests under rocks and natural burrows) ([Table A2](#)). And finally, we conducted colony-specific comparisons between the different nest types monitored at each of five colonies: (1) Bird Island (Cement, Ceramic, Fibreglass and Vegetation nests, in 2009–2014 and 2020–2022, [Table A2](#)); (2) Boulders Beach (Cement, Ceramic, Fibreglass and Vegetation nests, in 2020–2022, [Table A2](#)); (3) Dyer Island (Cement, Ceramic and Fibreglass, in 2018–2019 and 2021–2022, [Table A2](#)); (4) Robben Island (Fibreglass nest, other man-made structures, Vegetation nest and Wooden boxes in 2008–2022, [Table A3](#)); and (5) Stony Point (Cement, Ceramic, Fibreglass and Vegetation nests in 2019–2022, [Table A2](#)).

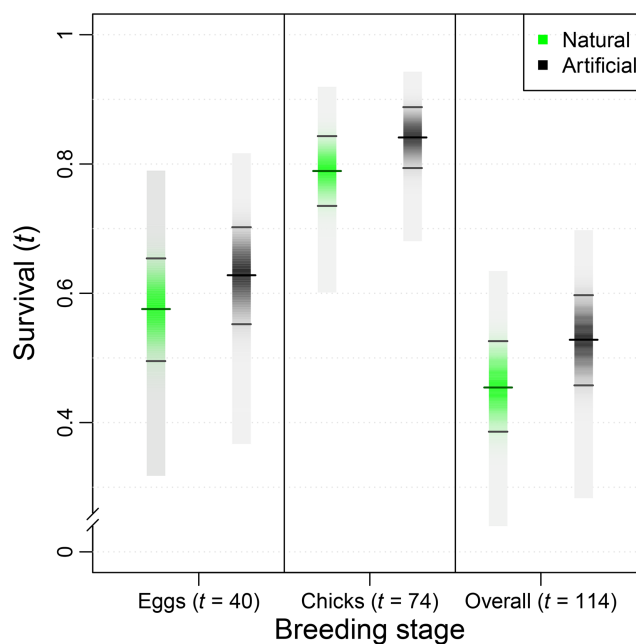
### 3 | RESULTS

#### 3.1 | Natural versus artificial nests

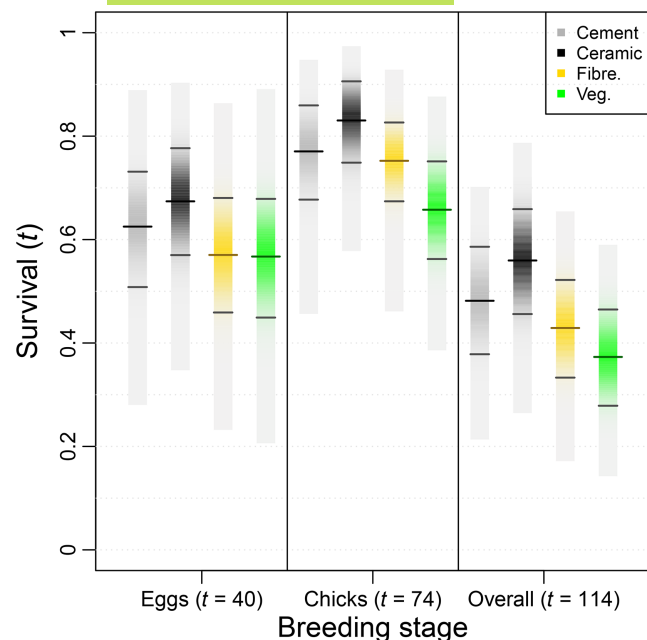
Overall, both egg and chick survival were credibly improved in artificial nests compared to natural nests (with  $> 99.5\%$  of the posterior distribution having the same sign as the mean). Egg survival (mean: 95% credible intervals) was 5.2 percentage points higher in all artificial nests (0.63: 0.55–0.70) than all natural nests (0.58: 0.50–0.65). Similarly, chick survival was 5.2 percentage points higher in artificial nests (0.84: 0.79–0.89) than in natural nests (0.79: 0.74–0.84); and the overall survival probability was 0.53 (0.46–0.60) in artificial nests and 0.45 (0.39–0.53) in natural nests ([Figure 3](#)), a difference of 7.4 percentage points or a 16.5 (6.7–26.2) % improvement from the natural nests baseline.

#### 3.2 | Four nest types across four colonies

When data collected from the four colonies for each of four nest types were combined, egg survival in ceramic nests (0.67: 0.51–0.73) was credibly higher than in vegetation nests (0.57: 0.45–0.68) and fibreglass nests (0.57: 0.46–0.68), but not in cement nests (0.63: 0.51–0.73; [Figure 4](#)).



**FIGURE 3** Modelled probability of African penguin egg survival at 40 days (left), chick survival at 74 days (middle) and overall breeding success (the survival probability for an individual egg to make it to a fledgling at 114 days post-laying; right) in two broad nest types, all artificial nests combined and all natural nests combined at eight colonies over 15 years (2008–2022). See [Table A1](#) for colony names and annual sample sizes at each colony in each nest type. Light grey polygons show the full posterior distributions, short tick marks are 95% credible intervals and long tick marks show the posterior mean.



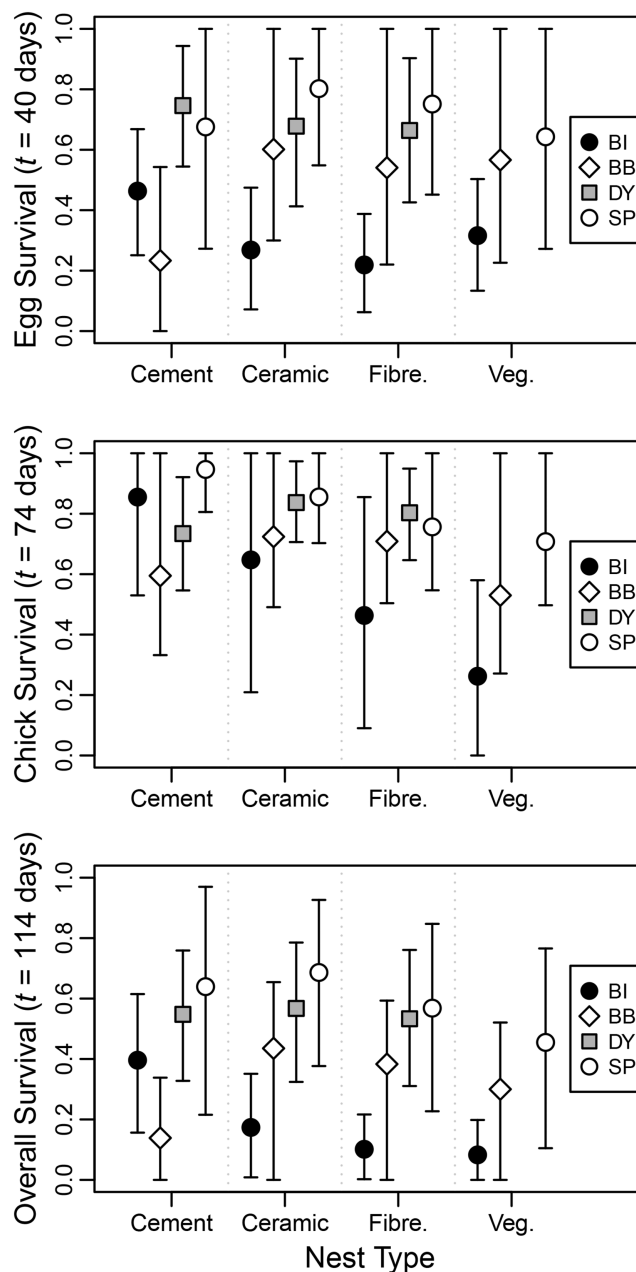
**FIGURE 4** Modelled survival probability of eggs (at 40 days), chicks (at 74 days) and overall breeding success (at 114 days) in the three artificial nest types (cement, ceramic and fibreglass nests) and vegetation nests monitored at four colonies (Bird Island, Boulders Beach, Dyer Island and Stony Point) over 15 years (2008–2022). See Table A2 for annual sample sizes at each colony in each nest type. Polygons and tick marks are as in Figure 3.

Mean chick survival was  $>0.75$  in the three artificial nest types and was credibly improved in all compared to vegetation nests (0.66: 0.56–0.75). Chick survival was highest in ceramic nests (0.83: 0.75–0.91), intermediate in cement nests (0.77: 0.68–0.86) and lowest in fibreglass nests (0.75: 0.67–0.83; Figure 4), but the variation in survival within artificial nest types meant it only differed credibly between ceramic and fibreglass nests.

Overall survival followed the same pattern as chick survival; it was credibly higher in all three artificial nest types than in vegetation nests (0.37: 0.28–0.46; Figure 4) and was also credibly higher in ceramic nests (0.56: 0.46–0.66) than in fibreglass nests (0.43: 0.33–0.52), with cement nests (0.48: 0.38–0.59) intermediate between and not credibly different from the two other artificial nest types.

### 3.3 | Colony level comparisons

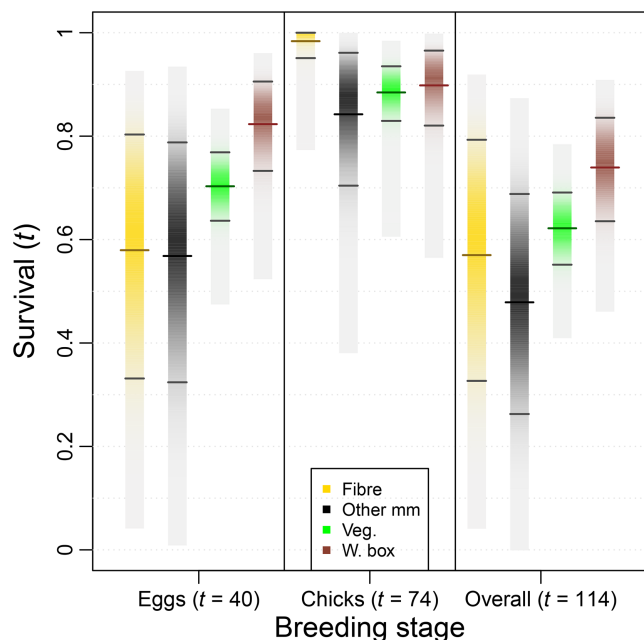
Breeding success varied extensively across colonies and year (Appendix S2) and the success of the various artificial nest types differed significantly between sites. In most cases, the survival rates were highly variable (high uncertainty in the estimates) and the efficacy of the different kinds of artificial nests in terms of improving breeding productivity relative to nests under vegetation was context specific. For example, the cement nests had the highest egg and chick survival rates at Bird Island, the highest chick survival rates



**FIGURE 5** Modelled survival probability (mean and 95% CI) of eggs (at 40 days), chicks (at 74 days) and overall breeding success (at 114 days) in the three artificial nest types (cement, ceramic and fibreglass nests) and vegetation nests broken down by colony (BB, Boulders Beach; BI, Bird Island; DY, Dyer Island; SP, Stony Point) where all nest types were monitored concomitantly (except for natural nests at Dyer Island). See Table A2 for annual sample sizes in each nest type at each colony.

at Stony Point and the highest egg survival at Dyer Island, but the lowest egg survival (by  $>30$  percentage points) at Boulders Beach (Figure 5). Ceramic nests had the highest egg and chick survival at Boulders Beach and egg survival at Stony Point. Fibreglass burrows generally performed less well than all other artificial nest types (but usually at least as well as or better than nest under vegetation), except at Robben Island where chick survival was the highest (albeit





**FIGURE 6** Modelled survival probability of eggs (at 40 days), chicks (at 74 days) and overall breeding success (at 114 days) in four nest types, fibreglass nests (yellow), other man-made nests (mostly old & disused buildings; black), vegetation nests (green) and wooden nest boxes (brown) at Robben Island over 15 years (2008–2022). See Table A3 for annual sample sizes in each nest type. Polygons and tick marks are as in Figure 3.

from a small sample size; Figure 6; Table A3). Vegetation nests were never the best nest type for either egg or chick survival at any colony (Figures 5 and 6).

### 3.3.1 | Bird Island

From a colony perspective, at Bird Island, survival in cement nests (eggs 0.46: 0.25–0.67; chicks 0.86: 0.53–1.00) was credibly higher for both eggs and chicks than in fibreglass (eggs 0.22: 0.06–0.39; chicks 0.46: 0.09–0.85) or vegetation nests (eggs 0.32: 0.13–0.50; chicks 0.26: 0.00–0.58), but not ceramic nests (eggs 0.27: 0.07–0.47; chicks 0.65: 0.21–1.00). Survival at Bird Island was two to five times higher in the cement nests than in any other nest type (Figure 5), although survival in all nest types was low overall ( $\leq 0.40$ ). In fact, while chick survival at Bird Island was generally low compared to other colonies, especially in natural and fibreglass nests, chick survival in cement nests was comparable (or even higher) to that of any nest type at other colonies (Figure 5).

### 3.3.2 | Boulders Beach

Survival was poorest in cement nests (0.23: 0.00–0.54) and credibly lower than the other three nest types, which varied little from 0.54 (0.22–1.00) in fibreglass burrows to 0.60 (0.30–1.00) in

ceramic nests (Figure 5). However, cement nests at Bird Island and at Boulders Beach are of different designs, hence not necessarily comparable. Chick survival at Boulders Beach varied from 0.53 (0.27–1.00) in vegetation nests to 0.72 (0.49–1.00) in ceramic nests but did not differ credibly between the four nest types. Almost in complete contrast to Bird Island, overall survival at Boulders Beach was two to three times higher in nest types other than the cement nests (Figure 5).

### 3.3.3 | Dyer Island

Here, there were too few vegetation nests to be included in the analysis, but neither egg nor chick survival differed credibly between the artificial nest types and the overall survival rates were similar between cement (0.55: 0.33–0.76), ceramic (0.57: 0.32–0.79) and fibreglass (0.53: 0.31–0.76) nests (Figure 5).

### 3.3.4 | Robben Island

Here, there were no cement nests and too few breeding attempts in ceramic nests to include that nest type, but egg survival was credibly higher in wooden boxes (0.82: 0.73–0.91) than in fibreglass burrows (0.58: 0.33–0.80) or 'Other man-made' nests (0.57: 0.32–0.79), and not credibly higher than nests under Vegetation (0.70: 0.64–0.77) (Figure 6). This value of 0.82 in wooden boxes was the highest long-term egg survival rate recorded in any nest type in this analysis (Figures 5 and 6). However, chick survival at Robben Island was credibly higher in fibreglass burrows (0.98: 0.95–1.00) than in the other three nest types, which ranged from 0.84 (0.70–0.96) in 'Other man-made' nests to 0.90 (0.82–0.97) in wooden boxes and did not differ credibly from one another (Figure 6). Overall mean survival was 12 percentage points better and credibly higher in wooden boxes (0.74: 0.64–0.84) than in nests under vegetation (0.62: 0.26–0.69), 26 percentage points better and credibly higher than nests in 'Other man-made' structures (0.48: 0.26–0.69) and 17 percentage points better than in fibreglass burrows, though the latter was not credibly different due to high variation in the fibreglass burrows (Figure 6).

### 3.3.5 | Stony point

Here, egg survival varied by 16 percentage points from 0.64 (0.27–1.00) in vegetation nests to 0.80 (0.55–1.00) in ceramic nests but did not differ credibly between any of the nest types (Figure 5). Chick survival was credibly higher in cement nests (0.95: 0.81–1.00) than fibreglass burrows (0.76: 0.55–1.00) and vegetation nests (0.71: 0.50–1.00), but not ceramic nests (0.86: 0.70–1.00). Overall survival ranged from 0.45 (0.10–0.77) in vegetation nests to 0.69 (0.38–0.93) in ceramic nests, but only this difference (between

vegetation and ceramic nests) differed credibly at the 95% level (Figure 5).

## 4 | DISCUSSION

Artificial nests have been deployed in African penguin colonies for decades and tested multiple times, but with mixed results depending on the colony and the type of nest tested (e.g. Hugo, 2021; Kemper et al., 2007; Pichegru, 2013; Sherley et al., 2012; Tol, 2016). When considering all types of designs across all colonies, over a 14-year period, artificial nests have positively impacted African penguins by increasing the breeding output of those birds breeding in them by 16.5% over naturally occurring nests. Artificial nests tend to improve chick survival compared to natural nests slightly more than egg survival (Figures 4 and 5). Chicks are generally more vulnerable to extreme weather events and predators than eggs (Seddon & van Heezik, 1993), and breeding failure at the chick rearing stage is less likely to be followed by another clutch (Randall & Randall, 1981). Therefore, increasing chick survival is likely to contribute proportionally more significantly to increased recruitment to the population than egg survival. Importantly, a 10% increase in African penguin chick survival following the exclusion of fishing close to Robben and Dassen Islands translated into ~0.7% improvement in population growth on the colonies (Sherley et al., 2018). Therefore, while only a portion of the South African penguin population breeds in artificial nests, the observed 16.5% increase breeding success will have likely slowed the rate of decline of this species across the country. This nation-wide conservation measure required coordination across multiple institutions for the deployment and consistent monitoring of these various nests over time. This cooperation facilitated the collection of extensive scientific data which allowed assessing the validity of this conservation action. This study demonstrated that artificial nests successfully contribute towards reducing the risks of extinction in the wild of this endangered species, the main goal of the African Penguin BMP (DEA, 2013), highlighting the value of multi-institutional cooperation in conservation.

While all natural nests combined were found to have a lower overall breeding success compared to artificial nests in this study, natural burrows are known to offer a constant microclimate with buffered temperatures and humidity levels, as well as protection against predators, providing an ideal environment for the brood (Frere et al., 1992). They may not have been outperformed by artificial nests if tested in isolation. But only very few of these natural burrows are still available to African penguins, which mostly breed in vegetation or surface nests. Natural nests monitored for breeding success are often chosen in easily accessible areas (i.e. more exposed) to reduce disturbance, but also possibly more vulnerable than nests in more densely vegetated areas. At Boulders Beach and Robben Island, for example, most natural nests are in dense vegetation, which may provide more shelter against sun exposure and high temperatures compared to open surface nests (Lei et al., 2014).

Chicks from open nests can also move away from their initial nest site into vegetated areas or join with others to form creches, making them more difficult to monitor accurately. Therefore, breeding success in natural nest may have been slightly underestimated in this study due to logistical challenges.

Nevertheless, artificial nests contributed to successfully increase local populations of African penguins, as has been found for other burrowing seabirds (e.g. storm petrels, Libois et al., 2012; or shearwaters, Bourgeois et al., 2015) or non-burrowing species (e.g. terns, Burke et al., 2022; Hart et al., 2016). For some, however, they were shown to significantly increase breeding output only during years of poor environmental conditions over a 25-year period (Sutherland et al., 2014). Often, flaws in designs, colours, smell or placement led to sub-optimal nesting conditions inside these nests, such as higher temperatures or increased parasite loads compared to natural nests (Zhang et al., 2023), with studies recommending improved designs to maximise conservation benefits at species level (see Zhang et al., 2023 for a review). The latest design of artificial nests for African penguins, the ceramic nests, developed under the auspices of the BMP (DEA, 2013), was generally the most successful at increasing breeding output compared to earlier designs, although not systematically (Figure 4). By investigating four different nest types at several colonies over a 14-year period in comparison to natural nests, we show that no single design of artificial nests for African penguins was consistently most effective across all sites. Consequently, as a conservation strategy to maximise African penguin breeding productivity, the deployment of artificial nests should be colony specific. Wooden boxes were the best performing nests on Robben Island (Figure 6), despite higher temperatures than natural nests (Sherley et al., 2012; Tol, 2016). Cement nests were the most successful on Bird Island (Figure 5), although they also had relatively high temperatures (Lei et al., 2014). But the type of cement nests deployed on that colony had wide openings on both sides (Figure 2c), which probably allowed for air flow to cool the nest. They may therefore not provide adequate protection against terrestrial predators and that specific design may not be the most appropriate in mainland colonies. Number of natural predators at the colony like Kelp Gulls *Larus dominicanus* are kept low by active management to limit predation (Pichegru, 2013), hence allowing open cement nests to be most suited there. Mammalian predators are responsible for significant mortalities in mainland colonies (Vanstreels et al., 2019) and to adequately protect eggs and chicks, artificial nests may need to be more enclosed. The most recent design (ceramic double-layered nests) was generally more successful at improving hatching and fledging success compared to natural nests or earlier designs of artificial nests (e.g. fibreglass nests), even if not consistently across colonies (Figure 5). Like fibreglass nests, ceramic nests had only one narrow opening (Figure 2), allowing protection against predators. However, the formers are known to have high ambient temperatures, detrimental to egg hatching in some cases (Lei et al., 2014; Sherley et al., 2012; Tol, 2016). By contrast, ambient temperatures in ceramic nests are lower than in other nest types

(Welman & Pichegru, 2022), thus making them potentially the most suited for mainland colonies.

However, increased parasite load is a recurrent issue in many artificial nest types for various avian species (Zhang et al., 2023) and prevalence of ectoparasites (mostly fleas and soft ticks) has been shown to be higher in fibreglass and cement nests for African Penguins at Stony Point compared to natural nests (Espinaze et al., 2020a). Ecto- and endoparasite infestation may affect adult and chick body condition (mass and haematocrit levels, Espinaze et al., 2020b), and parasite build-up can be rapid (i.e. within a single season, Carr, 2020). Therefore, methods to clean artificial nests or the possible use of eco-friendly pesticides should be explored to optimising nesting conditions for African penguins. Some hole-nesting bird species deliberately avoid nest boxes with high parasite loads (Breistol et al., 2015); thus, high ectoparasite presence could affect the reuse rate of artificial nests by African Penguins and should be investigated in future.

The very low breeding success observed in colonies in Algoa Bay and at Simon's Town (Figure 5; Appendix S2), especially in natural nests, remains extremely worrisome, and artificial nests alone cannot compensate for poor breeding conditions for penguins. Multiple conservation measures are in place in most colonies to improve wild African penguins' survival and breeding outputs (DFFE, 2013; Pichegru et al., in review). In addition to the placement of artificial nests, habitat restoration is also taking place by removing alien vegetation (Sherley et al., 2012), brush packing to protect nesting habitat from weather events or creating drainage to limit flooding. The quasi-systematic removal of abandoned eggs and chicks at various colonies (Klusener et al., 2018; Sherley et al., 2014) also proved successful in increasing the overall breeding population of African penguins in South Africa (Pichegru et al. in prep). In addition, the management of predators at sea (e.g. Cape fur seals *Arctocephalus pusillus pusillus*) and in the colony (e.g. kelp gulls or terrestrial predators on mainland colonies) is taking place at various locations and at various levels (Pichegru et al., in review; Pichegru, 2013). Disturbance from researchers, film crew and the public is also strictly minimised through sets of protocols and guidelines from government and colony management agencies (DEA, 2013), as well as public awareness campaigns (J. Mann, pers. comm.).

Even so, the continuous decline in numbers of African penguins over the recent decades calls for further urgent actions. Adult survival has decreased over recent decades from 0.81 ( $\pm 0.08$ ) during 1994–2001, to 0.61 ( $\pm 0.12$ ) during 2002–2012, and 0.77 ( $\pm 0.02$ ) during 2013–2020 at Robben Island (Leith et al., 2022; Sherley et al., 2014), largely in response to changing food availability (Crawford et al., 2011; Leith et al., 2022; Robinson et al., 2015). While improved breeding success in artificial nests likely contributes significantly towards slowing the decline of the species, repeated evidence of poor feeding conditions in the birds' foraging habitat (e.g. Crawford et al., 2019) underline calls for concrete actions to increase food availability for penguins, including biologically meaningful marine protected areas (Pichegru et al., 2010; Sherley et al., 2015,

2018; Sydeman et al., 2021) and wider ecosystem-based approaches to fisheries management (Shannon et al., 2010).

## AUTHOR CONTRIBUTIONS

Lorien Pichegru, Richard B. Sherley, Katta Ludynia, Barbara J. Barham and Lauren Waller led the writing of the manuscript and the analysis of the data. All authors collected data, contributed to the drafts of the manuscript and gave approval for publication.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1002/2688-8319.12388>.

## DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.pg4f4qzrw> (Pichegru et al., 2024).

## STATEMENT OF INCLUSION

Our study brings together authors from a number of different countries, most from the country where the study was carried out. All authors were engaged early on with the research and study design and their perspectives were considered. Literature published by scientists from the region was cited adequately.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix S1.** Sample size details.

**Appendix S2.** Breeding success.

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