



# Ostrich

Journal of African Ornithology

ISSN: 0030-6525 (Print) 1727-947X (Online) Journal homepage: [www.tandfonline.com/journals/tost20](http://www.tandfonline.com/journals/tost20)

## High adult mortality of African Penguins *Spheniscus demersus* in South Africa after 2004 was likely caused by starvation

Robert JM Crawford, Richard B Sherley, Lynne J Shannon, Alistair M McInnes, Tegan Carpenter-Kling & Azwianewi B Makhado

To cite this article: Robert JM Crawford, Richard B Sherley, Lynne J Shannon, Alistair M McInnes, Tegan Carpenter-Kling & Azwianewi B Makhado (04 Dec 2025): High adult mortality of African Penguins *Spheniscus demersus* in South Africa after 2004 was likely caused by starvation, Ostrich, DOI: [10.2989/00306525.2025.2568382](https://doi.org/10.2989/00306525.2025.2568382)

To link to this article: <https://doi.org/10.2989/00306525.2025.2568382>



© 2025 The Author(s). Co-published by NISC Pty (Ltd) and Informa UK Limited, trading as Taylor & Francis Group



Published online: 04 Dec 2025.



Submit your article to this journal [↗](#)



Article views: 191



View related articles [↗](#)



View Crossmark data [↗](#)

# High adult mortality of African Penguins *Spheniscus demersus* in South Africa after 2004 was likely caused by starvation

Robert JM Crawford<sup>1</sup> , Richard B Sherley<sup>2,3,4\*</sup> , Lynne J Shannon<sup>5</sup> , Alistair M McInnes<sup>6,7</sup> , Tegan Carpenter-Kling<sup>7</sup>  and Azwianewi B Makhado<sup>1,8,9</sup> 

<sup>1</sup> Oceans and Coasts Branch, Department of Forestry, Fisheries and the Environment, Cape Town, South Africa

<sup>2</sup> Environment and Sustainability Institute/Centre for Ecology and Conservation, University of Exeter, Penryn, United Kingdom

<sup>3</sup> Department of Biodiversity and Conservation Biology, University of the Western Cape, Cape Town, South Africa

<sup>4</sup> College of Marine Sciences and Aquatic Biology, University of Khorfakkan, Sharjah, United Arab Emirates

<sup>5</sup> Department of Biological Sciences, University of Cape Town, Cape Town, South Africa

<sup>6</sup> Seabird Conservation Programme, BirdLife South Africa, Cape Town, South Africa

<sup>7</sup> Institute for Coastal and Marine Research, Nelson Mandela University, Gqeberha, South Africa

<sup>8</sup> FitzPatrick Institute of African Ornithology, University of Cape Town, Cape Town, South Africa

<sup>9</sup> Polar Research Institute of China, Shanghai Ocean University, Shanghai, China

\* Correspondence: [r.sherley@exeter.ac.uk](mailto:r.sherley@exeter.ac.uk)

From 2004–2011, following the collapse of sardine *Sardinops sagax*, a main food for African Penguins *Spheniscus demersus*, to < 25% of its maximum recorded abundance, survival of penguins breeding at Dassen and Robben islands, north of Cape Town, South Africa decreased markedly. Based on numbers of penguins breeding at the two islands and observed increased levels of mortality, it was estimated that ~62 000 breeding individuals (~95% of the birds that elected to breed in 2004) died as a result of food scarcity in this eight-year period. African Penguins moult annually, coming ashore and fasting for 21 days, when they shed and replace all their feathers. Failure to fatten sufficiently to moult, or to regain condition afterwards, results in death. At both islands, annual survival rates of adult penguins, and proportions of breeders that failed to return to their colonies to moult, were significantly related to an index of prey availability developed for the region. Although some adults moulted at a colony to the southeast, where food may have been more plentiful, much of the mortality likely resulted from failure of birds to fatten sufficiently to moult. The fishery exploitation rate of sardines west of Cape Agulhas was consistently above 20% between 2005 and 2010, peaking at 80% in 2006. In 2024, African Penguins were uplisted to Critically Endangered on the IUCN Red List. Management that helps to promote the long-term recovery of sardine biomass in the main foraging areas of African Penguins throughout their annual cycle will be important in securing their future survival.

## Famine comme la cause la plus probable de la mortalité élevée d'adultes de Manchots du Cap *Spheniscus demersus* en Afrique du Sud après 2004

De 2004 à 2011, à la suite de l'effondrement des stocks de sardines *Sardinops sagax*, principale source de nourriture des Manchots du Cap *Spheniscus demersus*, qui ont chuté à moins de 25 % de leur abondance maximale, la survie des manchots se reproduisant sur les îles Dassen et Robben, au nord du Cap, en Afrique du Sud, a considérablement diminué. Sur la base du nombre de manchots se reproduisant sur les deux îles et de l'augmentation observée des taux de mortalité, on estime qu'environ 62 000 individus reproducteurs (soit environ 95 % des oiseaux qui avaient choisi de se reproduire en 2004) sont morts en raison de la pénurie alimentaire au cours de cette période de huit ans. Les manchots africains muent chaque année, venant à terre et jeûnant pendant 21 jours, pendant lesquels ils perdent et remplacent toutes leurs plumes. S'ils ne parviennent pas à s'engraisser suffisamment pour muer ou à retrouver leur condition physique après la mue, ils meurent. Sur les deux îles, les taux de survie annuels des manchots adultes et la proportion de reproducteurs qui n'ont pas réussi à retourner dans leurs colonies pour muer étaient étroitement liés à un indice de disponibilité des proies élaboré pour la région. Bien que certains adultes aient mué dans une colonie située au sud-est, où la nourriture était peut-être plus abondante, une grande partie de la mortalité était probablement due au fait que les oiseaux n'avaient pas réussi à s'engraisser suffisamment pour muer. Le taux d'exploitation de la sardine à l'ouest du cap Agulhas a été constamment supérieur à 20 % entre 2005 et 2010, atteignant un pic de 80 % en 2006. En 2024, les Manchots du Cap ont été reclassés dans la catégorie 'en danger critique d'extinction' sur la Liste rouge de l'IUCN. Une gestion qui contribue à favoriser la reconstitution à long terme de la biomasse de sardines dans les principales zones d'alimentation des Manchots du Cap tout au long de leur cycle annuel sera importante pour assurer leur survie future.

**Keywords:** Benguela ecosystem, natural resource management, seabird conservation

## Introduction

The number of African Penguins *Spheniscus demersus* breeding in South Africa collapsed from ~56 000 pairs in 2001 to ~21 000 pairs in 2009, a loss of ~35 000 pairs (70 000 breeders, > 60% population decline) in eight years. Of these 35 000 pairs, ~11 000 (22 000 breeders) were lost from the Eastern Cape and ~24 000 (48 000 breeders) were lost from the Western Cape (Crawford et al. 2011). When including Namibian birds, this reduced the global population to 26 000 pairs, and led to classification of the species as Endangered in 2010 (BirdLife International 2024). In 2024, following further decreases in South Africa and Namibia, the species was subsequently uplisted to Critically Endangered (BirdLife International 2024; Sherley et al. 2024).

The decrease of penguins in the Eastern Cape in the early 2000s coincided with both an increased catch of sardine *Sardinops sagax* in that region and construction of the Coega harbour (Figure 1), making it difficult to ascribe losses to a specific cause (Crawford et al. 2009). In African Penguins, food availability has been linked to survival (both immature and adult, Sherley et al. 2014a), age at first breeding (Whittington et al. 2005a), participation in breeding (Crawford et al. 1999) and breeding success (e.g. Crawford et al. 2006a; Cury et al. 2011). The population decrease in the Western Cape this century was underpinned mainly by increased mortality of mature adults attributed to food scarcity (e.g. Crawford et al. 2011, 2022; Sherley et al. 2014a; Weller et al. 2014). In particular, South Africa's stock of sardine was below the long-term (1984–2022) mean biomass of 820 000 t for this species in 15 of the 18 years (83%) between 2005 and 2023 (excluding 2021, when no survey was made) (Coetzee and de Moor 2024). For 12 of those years (66%), it was below 500 000 t, including 'extreme lows of about 250 000 t in 2016 and 2020, about 190 000 t in 2019 and a thirty-year low of only 91 000 t in 2018' (Coetzee and de Moor 2024, p 6). Moreover, the biomass of sardine found to the west of Cape Agulhas — close to the once large seabird colonies of the Western Cape — has been below 336 000 t, or 25% of the maximum value observed west of Cape Agulhas of ~1.34 million t (Robinson et al. 2015), for all but two years since 2004 (see Figure 12 of Coetzee and de Moor 2024). This 25% value has been identified as a threshold beneath which survival of adult penguins at Robben Island decreased markedly (Robinson et al. 2015). In estimating the relative impacts of bottom-up (e.g. food) and top-down (e.g. predation) control on African Penguins in the Western Cape, Crawford et al. (2018) noted that colonies in that province were well monitored in the early 21st century so that losses could reasonably be apportioned to different causes. They deducted mortality attributable to factors other than food<sup>1</sup>, assumed that the balance resulted from insufficient prey availability and concluded that ~45 250 breeders were likely lost as a result of food scarcity.

<sup>1</sup> Cape Fur Seals *Arctocephalus pusillus pusillus* were estimated to have killed c. 2 400 adult African Penguins at Dyer Island between 2001 and 2009. In the same period, at least 324 penguins died as a result of oiling (Crawford et al. 2018).

In this paper, we further explore the impact of food availability on numbers of African Penguins at Dassen and Robben islands to the north of Cape Town (Figure 1) in the early 21st century, and attempt to identify the stage in the penguins' annual cycle at which birds were most susceptible to depleted prey resources. Underhill et al. (2006) found that penguin numbers at different colonies, such as Dassen and Robben islands, tended to rise and fall in similar ways, and these patterns were linked to food availability. In this study, we update the data from these two islands to see if their population trends continued to follow the same pattern up to 2015.

## Methods

### Data

We used counts of numbers of breeding pairs of African Penguins (Crawford et al. 2011; Makhado et al. 2025) and of numbers of adult-plumaged penguins moulting (Underhill and Crawford 1999; Wolfaardt et al. 2009; Robinson et al. 2015; updated by data held by the Department of Forestry, Fisheries and the Environment (DFFE) from monitoring conducted by DFFE and CapeNature) at Dassen and Robben islands for 1995–2015; and estimates of annual adult survival of penguins ( $\phi_a$ ) made at both islands using capture-mark-recapture (CMR) analyses for 2004–2011 (Sherley et al. 2014a). Most adult penguins at Dassen and Robben islands moult between November and January (Crawford et al. 2006b), so that counts of moulting birds for year  $t$  spanned the split year  $t/t + 1$ . At Dassen Island, counts of moulters are underestimates because many penguins moult in burrows (Wolfaardt et al. 2009). We assumed that the proportion of moulters not counted remained constant across years.

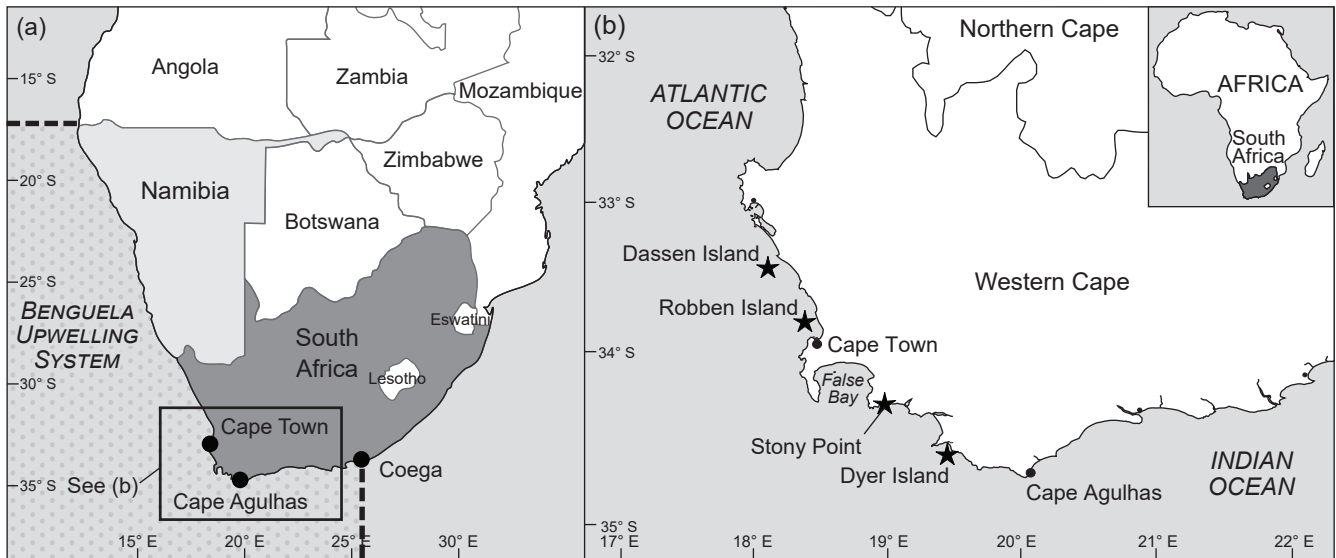
### Analyses

Robinson et al. (2015) showed that when South Africa's stock of sardine west of Cape Agulhas fell below 25% of its maximum observed biomass, adult survival ( $\phi_{a,R}$ ) at Robben Island decreased from a value of c. 0.87 p.a. to markedly lower levels. A similar response was found by Sherley et al. (2014a) at both our focal islands. The mean adult survival rate between 1994/95 and 2001/02 at Dassen Island was 0.78 p.a., while at Robben Island it was 0.84 (Sherley et al. 2014a). At both colonies  $\phi_a$  averaged 0.59 p.a. between 2004/05 and 2011/12 (Sherley et al. 2014a), when the sardine biomass off west South Africa was < 25% of its maximum value (Robinson et al. 2015).

We estimated the increase in adult mortality associated with food scarcity at both Dassen Island ( $\Delta M_{a,D,t}$ ) and Robben Island ( $\Delta M_{a,R,t}$ ) in the years ( $t$ ) 2004–2011 (i.e. after the biomass of sardine fell below the threshold of 25% of its maximum) as:

$$\begin{aligned}\Delta M_{a,D,t} &= 0.78 - \phi_{a,D,t} \\ \Delta M_{a,R,t} &= 0.84 - \phi_{a,R,t}\end{aligned}\quad (\text{Eqn. 1})$$

where 0.78 and 0.84 were the 1994/95–2001/02 mean survival rates for Dassen and Robben islands, respectively



**Figure 1:** The positions of localities mentioned in the text (circles; a) and of four African Penguin *Spheniscus demersus* breeding colonies off southwest South Africa (stars; b). The northern and eastern boundaries of the Benguela Upwelling System are indicated by the dashed lines in (a)

(from Sherley et al. 2014a, see above) and  $\phi_{a,D,t}$  and  $\phi_{a,R,t}$  were the island-specific annual estimates of  $\phi_a$  from Sherley et al. (2014a) for 2004/05 to 2011/12. This gives the excess mortality relative to baseline survival at each site. We then estimated the number of additional adult deaths attributable to low sardine biomass ( $\Delta D$ ) at each island as:

$$\Delta D_{i,t} = 2 \cdot P_{i,t} \cdot \Delta M_{a,i,t} \quad (\text{Eqn. 2})$$

where  $P_{i,t}$  is the number of pairs breeding at island  $i$  in year  $t$ , and each pair is assumed to represent two adults. Summing the values of  $\Delta D_{i,t}$  over 2004–2011 provided an estimate of the loss of breeding penguins attributable to reduced food availability in that period.

Finally, for the period 1995–2015, we used the numbers of breeding pairs ( $P_{i,t}$ ) and counts of adult-plumaged birds that later moulted ( $F_{i,t}$ ) to estimate the proportion of breeders that failed to moult at their nesting colonies after breeding as:

$$MM_{i,t} = (2 \cdot P_{i,t} - F_{i,t}) / (2 \cdot P_{i,t}) \quad (\text{Eqn. 3})$$

This proportion ('MM' = missing moults) may reflect birds that died, deferred moult (e.g. Kemper et al. 2008) or moulted away from the colony (e.g. Whittington et al. 2005b; Carpenter-Kling et al. 2022).

Crawford et al. (2019) used a principal component analysis of monthly information on the diet composition of Cape Gannets *Morus capensis* at two colonies to develop an index of the availability to seabirds of sardine and anchovy *Engraulis capensis*, termed forage availability index (FAI), off west South Africa for 1995–2015. We investigated the relationship between  $MM_{i,t}$  and  $FAI_t$  for both Dassen and Robben islands, anticipating that it would be negative if breeders died between the onset of breeding and the feather-shedding phase of moult or moved to other localities to moult (Whittington et al. 2005b; Carpenter-Kling et al. 2022), on account of food scarcity near the islands.

Because we previously detected non-linear relationships between the FAI and numbers of seabirds in South Africa (Crawford et al. 2019), we used the 'gamm' function from the *mgcv* library (v. 1.9-1; Wood 2003, 2017) for R (v. 4.4.3; R Core Team 2025) to fit a generalised additive model (GAM) of the form:

$$MM_{i,t} = \alpha + S(X_t) + \varepsilon_{i,t} \quad (\text{Eqn. 4})$$

where  $MM_{i,t}$  was the proportion of missing moults (Eqn. 3) at colony  $i$  in year  $t$ ;  $\alpha$  is the intercept;  $S(X_t)$  is a non-parametric smoothing function, specifying the shape of the effect of the forage availability index (FAI) on  $MM_{i,t}$ , and  $\varepsilon_{i,t}$  is a normally distributed error term ( $N(0, \sigma^2)$ ), with the  $\sigma^2$  estimated from the data. We used thin plate regression splines (Wood 2003) and allowed the degrees of freedom of the smoothing function to be selected automatically by generalised cross-validation (GCV), with the option for the function to be linear (e.g.  $S(X_t) = \beta \times X_t$ , where  $\beta$  is the slope).

For 1995–2014, for both islands we also examined the relationship between adults moulting in the split-year  $t/t + 1$  and numbers breeding in year  $t + 1$ . We thought it unlikely that substantial enhanced mortality would have occurred after the birds had successfully moulted in a given year, so we expected these relationships to be linear and positive because numbers moulting should provide a good prediction of numbers breeding. We therefore initially assessed these relationships using linear models ('lm' function in R). For each model (GAMs and linear models), we assessed residual plots for normality and heterogeneity of variance and checked for an absence of autocorrelation using the 'acf' function for autocorrelation plots and the 'dwtest' function from the *lmtest* library (v. 0.9-40; Zeileis and Hothorn 2002) to conduct the Durbin-Watson test (Durbin and Watson 1950, 1951). Both linear models showed evidence of significant first-order autocorrelation



in their residuals. We therefore refit these models using the 'hildreth.lu' function from the *HoRM* library (v. 0.1.3; Young 2017) in R to implement the Hildreth-Lu estimation (Hildreth and Lu 1960), with  $\rho = 0.36$  at Dassen Island and  $\rho = 0.44$  at Robben Island sufficient to clearly remove the evidence of first-order autocorrelation in the residuals (Durbin-Watson  $p > 0.1$ ).

And, lastly, Underhill et al. (2006) showed that African Penguin populations at different colonies in the same region tended to fluctuate in similar ways over time ('regional coherence'). To test whether this coherence persisted, we calculated Pearson's correlation coefficients for the number of breeding pairs, adult moulters and missing moulters at Dassen and Robben islands from 2000 to 2015.

## Results

Over the eight-year period 2004–2011, the additional mortality of breeding African Penguins, estimated to have arisen as a result of depletion of the sardine biomass to below 25% of its maximum value (the threshold beneath which mortality increased, Robinson et al. 2015), was 44 602 and 17 155 individuals at Dassen and Robben islands, respectively. This amounted to ~62 000 adult penguins, or the equivalent of ~95% of the ~65 000 individuals that bred at these islands in 2004.

For 1995–2015, at both Dassen and Robben islands the proportion of breeders that failed to moult at their nesting colonies after breeding was non-linearly related to the FAI (Figure 2). At Dassen Island, the proportion of missing moulters was consistently above 0.6 when the FAI was negative (from 2003 to 2015) and below 0.6 when it was positive (1995 to 2002). At Robben Island, the pattern was similar, but the transition between positive and negative FAI phases was less clear. The proportion of missing moulters at Robben Island was predominately positive while the FAI was negative, with one exception in 2003, and negative in six of the eight years when the FAI was positive – the exceptions being 2001 and 2002, the years of the two highest FAI values.

Over the period 1995/96 to 2015/16, numbers of adult penguins moulting in split year  $t/t + 1$  were significantly positively related to those breeding in year  $t + 1$  for both Dassen ( $n = 21$ , adjusted  $r^2 = 0.631$ ,  $F_{1,17} = 31.8$ ,  $p < 0.001$ ) and Robben ( $n = 21$ , adjusted  $r^2 = 0.626$ ,  $F_{1,17} = 31.1$ ,  $p < 0.001$ ) islands based on the Hildreth-Lu estimation (Figure 3).

For 2000–2015, numbers of African Penguins breeding at Dassen and Robben islands were significantly correlated with each other ( $n = 16$ ,  $r = 0.957$ ,  $p < 0.001$ ). This was also the case for numbers of adult penguins moulting at the islands ( $n = 16$ ,  $r = 0.918$ ,  $p < 0.001$ ) and the proportions of breeders that subsequently missed moult ( $n = 16$ ,  $r = 0.722$ ,  $p = 0.002$ ).

## Discussion

### Starvation-induced mortality

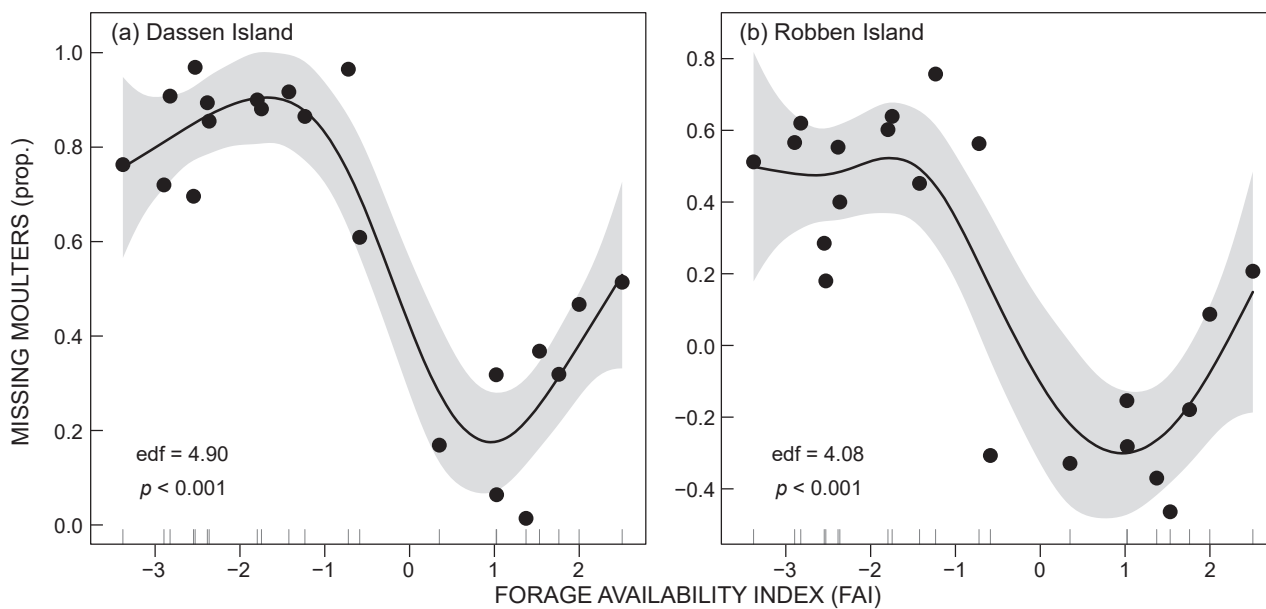
In 2004, at the start of the period considered in this study, ~65 400 African Penguins elected to breed at Dassen and Robben islands (~32 700 pairs), and about 108 000 penguins (~54 000 pairs) did so across the species

breeding range (see Sherley et al. 2024). Our calculations suggest that in the eight-year period from 2004 to 2011, ~62 000 of those birds breeding at Dassen and Robben islands died as a consequence of South Africa's sardine resource located to the west of Cape Agulhas collapsing below, and remaining less than, 25% of the maximum observed value in that region (i.e. ~336 000 tonnes). Breeding African Penguins show high fidelity to mates and hence to colonies (Randall 1983; Crawford et al. 1995), which exposes them to risk of local prey depletion. Age at first breeding of African Penguins is usually 4–6 years, and dependent on food supplies (Whittington et al. 2005a), and the proportion of sexually mature birds that breed is also related to prey availability (Crawford et al. 1999). Thus the number of adult-plumaged penguins that died as a result of food scarcity may have been larger. Regardless, it was more than the loss of ~45 250 breeders estimated for South Africa's Western Cape for 2001–2009 (Crawford et al. 2018). This discrepancy results from the different geographical extents of the studies, and because numbers of penguins breeding at both Dassen and Robben islands increased between 2001 and 2004 but decreased from 2009 to 2011 (Makhado et al. 2025).

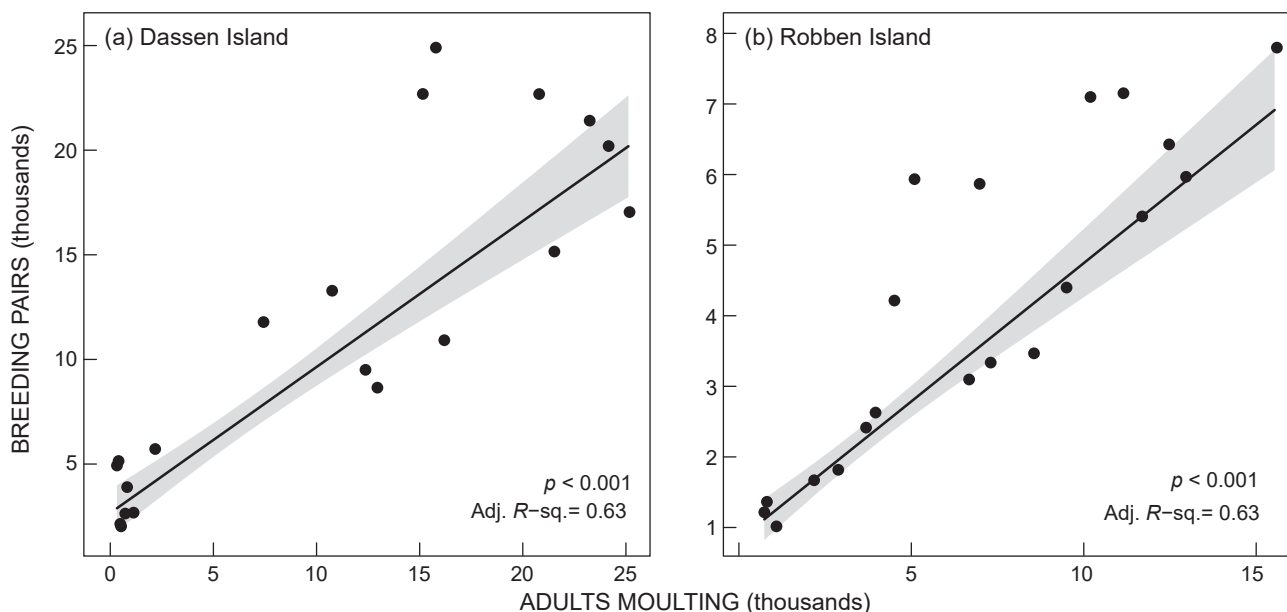
In 2000, the *Treasure* sank between Dassen and Robben islands and oil from that ship washed ashore on penguin landing beaches at both islands. About 19 000 oiled penguins were collected for cleaning, care and subsequent return to the wild (~2 000 died in captivity), and ~19 500 unoiled penguins were relocated to prevent them becoming oiled (Crawford et al. 2000). Deplorably, our results underline that the number of adult penguins lost shortly afterwards at Dassen and Robben islands through food scarcity was > 1.5 times the quantity saved by the rescue operation. Further, it is sobering that the number of breeders lost to food scarcity at Dassen and Robben islands from 2004–2011 was approximately three times larger than the global population of African Penguins remaining in 2023 (~19 800 breeders; Sherley et al. 2024).

### The vulnerable moult period

African Penguins undergo a catastrophic moult each year, usually shortly after the conclusion of their breeding season (Randall and Randall 1981; Kemper et al. 2008). During moult, they come ashore for about 21 days to shed and replace all their feathers at once (Randall and Randall 1981). Penguins need to moult approximately annually (Randall and Randall 1981; Kemper et al. 2008) because both the insulation and hydrodynamic capacity of feathers degrades over time. Penguins with year-old plumage (i.e. those about to moult) have a top underwater swimming speed of about 14 km h<sup>-1</sup>, compared to about 19 km h<sup>-1</sup> with new plumage (Wilson 1985), and likely have higher metabolic costs of swimming from the additional drag and poorer insulation. While ashore moulters also fast, losing ~47% of their body mass, part of which is substantial atrophy of the pectoralis and supracoracoideus muscles that power swimming. So, although their feathers are in excellent condition immediately post-moult, the muscle atrophy means they may temporarily be able to obtain maximum swimming speeds of only around 10 km h<sup>-1</sup>, about the same top speed as their preferred



**Figure 2:** Results of generalised additive model fits of the relationship between the proportion of missing African Penguin *Spheniscus demersus* moulters (breeders that failed to moult at their nesting colonies after breeding) and the *Forage Availability Index (FAI)* from Crawford et al. (2019) (the FAI represents the combined contribution of sardine and anchovy to the diet of Cape Gannets) at Dassen Island (top) and Robben Island (bottom), South Africa, 1995–2015. The estimated degrees of freedom (edf) of the smoothing term for each model is given on the plot. The grey shading shows pointwise 95% confidence intervals and circles show the observations (partial residuals around the significant covariate effects)



**Figure 3:** The linear relationships (black line) and 95% confidence intervals (grey polygon) between numbers of adult African Penguins *Spheniscus demersus* moulting in split-year  $t/t + 1$  and the numbers of pairs breeding in year  $t + 1$  at Dassen (top) and Robben (bottom) islands, South Africa, 1995/96–2015/16, derived from models fit using the Hildreth-Lu estimation, with  $\rho = 0.36$  at Dassen and  $\rho = 0.44$  at Robben, to remove serial autocorrelation from the residuals

prey (Wilson 1985). Penguins must therefore fatten at sea beforehand and rebuild condition afterwards for ~35 and 42 days pre- and post-moult, respectively (Randall 1983, 1989; Adams and Brown 1990). Pre-moult adults are on average 31% heavier than breeding adults (Cooper 1978)

and failure to fatten sufficiently for the energetically costly moult, or to regain condition afterwards, results in death (Morgenthaler et al. 2018; Carpenter-Kling et al. 2022). Hence, moult is a critical period in their annual cycle (Wolfaardt et al. 2009) and birds needing to prepare for

moult will abandon breeding attempts, including unfledged chicks, in order to fatten (Sherley et al. 2014b).

### **Estimating mortality from missing moulters**

The feather-shedding phase of moult lasts about 12.7 days in African Penguins (Randall 1983), so counts of penguins moulting feathers at intervals of ~12.7 days can provide an estimate of numbers moulting at a locality (Randall et al. 1986), especially when moult timing is quite synchronous and birds are highly visible, e.g. congregating at the coast to drink or preen, as was the case at Robben Island until 2004 (Underhill and Crawford 1999; Crawford et al. 2006b; Mdluli and Barham 2022). Although mature penguins will not necessarily breed every year (Leith et al. 2022), as noted above, they need to moult to survive and the majority have historically moulted at their breeding islands (Randall et al. 1986, Whittington et al. 2005b). The negative values of missing moulters (MM) at Robben Island between 1995 and 2000 broadly coincided with the positive phase of the food availability index (FAI; 1995–2002, Figure 2) and indicates that more adults moulted at the island than bred in the preceding nesting season. This suggests that the majority of breeders subsequently moulted at Robben Island in these years, along with a number of mature birds that had elected not to breed that season, or were unable to get into sufficient body condition to breed, or substantial numbers of adult-plumaged pre-breeders. Similarly, although the MM proportions were never negative at Dassen Island (because many penguins moult in burrows there; Wolfaardt et al. 2009), the clear distinction in the proportions of missing moulters when the FAI was positive (1995 to 2002,  $MM < 0.6$ ) from when it was negative (from 2003 to 2015,  $MM > 0.6$ ; Figure 2) also suggests that there was insufficient food near these islands for many breeders to fatten in their vicinity after 2002.

It is also worth noting that some of the MM in our dataset could have been due to birds choosing to moult elsewhere, particularly towards the end of our time-series. Only 50% of pre-moult birds tracked from Dassen Island between 2012 and 2019 moulted at the island; the other half moulted at Stony Point 150 km to the southeast. Some travelled to the east of Cape Agulhas to fatten (Carpenter-Kling et al. 2022). No unusual mortality or strandings of emaciated birds were observed ashore at either colony or on the continental mainland (Crawford et al. 2018) as has been seen in, for example, Southern Rockhopper Penguins *Eudyptes chrysocome* (Morgenthaler et al. 2018). Nevertheless, between 1994/1995 and 2011/2012, survival of adult African Penguins at Dassen and Robben islands was positively related to the FAI, which, unfortunately for seabirds off west South Africa remained low until at least 2015 (Crawford et al. 2019). This suggests that a dearth of food near Dassen and Robben islands likely caused substantial mortality of pre-moulters at sea.

### **Food availability for pre- and post-moulted birds**

The positive relationships between numbers of adult penguins moulting and those later breeding for both Dassen and Robben islands (Figure 3) suggest most penguins that successfully moulted were subsequently able to regain body condition and return to colonies to nest, in contrast to

the MM (birds that bred but then failed to appear in moult counts), which appear to have most likely died as a result of starvation (Figure 2). This further underpins the critical importance of good food availability for penguins pre-moult to attain sufficient body condition to make it through the moult fast, something also noted in other species, including Adelié *Pygoscelis adeliae*, Little *Eudyptula minor*, and Southern Rockhopper Penguins (Gales et al. 1988; Southwell et al. 2015; Morgenthaler et al. 2018). Equally, birds need a reliable food resource close to the moulting location immediately after moult, when their body mass is critically low (Kooyman et al. 2004).

The positive relationships between numbers of adult penguins at Dassen and Robben islands that bred, moulted or failed to return to moult imply these trends were influenced by factors that operated at a regional rather than island-specific scale, corroborating previous findings for 1996–2005 (Underhill et al. 2006). Availability of food to seabirds in the Benguela upwelling system may be influenced by environmental perturbations, e.g. Benguela Niños (Crawford et al. 2007), or other natural factors that displace fish stocks away from colonies (Crawford et al. 2015), and by fishing pressure that depletes local or regional prey availability. The harvest proportion (fishing pressure) of sardine west of Cape Agulhas was consistently above 20% (including small sardine bycatch) between 2005 and 2010, sometimes markedly so (peaking at 80% in 2006; Coetzee and de Moor 2024). High regional exploitation rates give rise to the potential for localised fisheries' impacts on dependent predators. For example, 70 000 tonnes of sardine were caught within 30 km of Dyer Island in 2004 and, when the size of that African Penguin colony was > 3 500 pairs, numbers breeding were negatively related to sardine catches made within 20 nautical miles of it (Ludynia et al. 2014).

### **Management measures**

In 2020, a Benguela Current Forage Fish Workshop, held under the auspices of the Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA), an intergovernmental treaty to which South Africa is a party, recommended development of 'a toolbox for the flexible and spatially appropriate management of forage fish in relation to threatened endemic Benguela seabird species in an effort to increase the availability of sufficient forage fish in key foraging areas throughout the annual cycle, including consideration of applicable management and conservation options, such as:

- Setting ecosystem thresholds, i.e. sizes of forage resource populations below which a range of precautionary measures relating to fishing would be implemented at various spatial scales;
- Closing of key foraging areas to fishing adjacent to major seabird colonies during the critical stages of their life cycle;
- Implementing spatial management of fishing pressure in important foraging areas for non-breeding seabirds' (AEWA 2020, p 3).

In 2023, an international expert panel reviewing results from experimental fishing closures adjacent to African Penguin breeding colonies noted that these closed areas were likely to have a positive impact on population growth

rates and that 'Future closures of forage-fish fishing around penguin colonies would be likely to benefit penguin conservation, but should be part of a larger package of conservation measures as such closures alone would be unlikely to reverse the current decline in penguin population numbers' (Punt et al. 2023, p 23).

Later the same year, South Africa's Minister of Forestry, Fisheries and the Environment implemented no-take fishing zones around six African Penguin colonies that held 76% of the species' global population, but their spatial extent was assessed as 'having little benefit to the African Penguin and little to no cost to the purse-seine fishery' (McInnes et al. 2024, p 1632). Consequently, in 2025, after a settlement between the conservation and fishing industry sectors was made an official order of the South African High Court, the Minister of Forestry, Fisheries and the Environment amended the extents of the closures to take better account of the foraging ranges of the penguins. It is hoped that the revised closures – which will operate year-round until at least 2033 – will decrease mortality of African Penguins and improve their breeding success at the six colonies around which they have been implemented. However, in the face of the ongoing impact of climate change on the abundance and distribution of their key prey, other interventions are likely to be needed (Punt et al. 2023), including those recommended by AEWA (2020) concerned with broader spatial management of fishing pressure. Comparison of fish community indicators west and east of Cape Agulhas additionally draws attention to the need for spatial management of fishing pressure (Shannon et al. 2024). Management of fishing pressure should also take account of the larger proportion of prey stocks consumed by predators at low levels of prey biomass (Saroux et al. 2021) and explore whether the current Operational Management Procedures employed by DFFE to allocate sardine and anchovy catches are adequately precautionary to the foraging needs of African Penguins (Punt et al. 2023).

With the global population falling to less than 10 000 pairs for the first time in 2023, it is now critical to make every effort to avert further reductions in colony sizes of African Penguins. Empirical information demonstrates that the probability of colony extinction increases as colonies get smaller (Crawford et al. 2001), *inter alia* because small colonies suffer from Allee effects (reduced fitness at low population sizes increasing extinction risk; e.g. Ryan et al. 2012). For example, African Penguins that feed in groups have a higher catch of prey per unit effort than solitary birds (McInnes et al. 2017), but colonies may become too small for sufficient foraging groups to form (Ryan et al. 2012). The fishing closures around the six African Penguin colonies, and broader-scale management of fishing pressure on South Africa's sardine and anchovy resources, will help offset colony decreases, and should also benefit the two other seabirds endemic to the region that depend on sardine and anchovy: Cape Gannet, which has undergone a population decline consistent with a global conservation status of Vulnerable (Sherley et al. 2019; Pistorius 2025) and Cape Cormorant *Phalacrocorax capensis*, which is considered Endangered in South Africa (McInnes et al. 2025).

**Acknowledgments** — We thank CapeNature and Robben Island Museum for permission to carry out research on the islands, accommodation and transportation to the islands; in particular, Sabelo Madlala, Inga Sipuka, T Mario Leshoro, Johan Visagie and Marlene van Onselen supported the fieldwork or contributed to data collection. We thank Sue Kuyper and our institutions for logistical support, and Peter and Barbara Barham, Nola Parsons, Leshia Upfold and Bruce Dyer, as well as numerous students, volunteers and collaborators that have helped with penguin fieldwork and data collection at both islands over the years. Funding for the long-term monitoring on Robben Island was provided by the Association of Zoos and Aquariums (through their SAFE programme), the Bristol Zoological Society, the Earthwatch Institute (<http://earthwatch.org/>), the Leiden Conservation Foundation, SANCCOB, the San Diego Zoo Wildlife Alliance and our institutes.

**Data availability** — The data used in this publication are available on the Figshare repository: <http://doi.org/10.6084/m9.figshare.28846445>, and from the authors upon reasonable request.

**Competing interests statement** — RBS and RJMC previously served on the Editorial Board of *Ostrich*. RBS is on the Board of Directors of SANCCOB, a registered non-profit company that receives donations and other funding for work on the conservation of seabirds, including the African Penguin.

## ORCID

Robert JM Crawford: <https://orcid.org/0000-0002-6566-6271>  
 Richard B Sherley: <https://orcid.org/0000-0001-7367-9315>  
 Lynne J Shannon: <https://orcid.org/0000-0001-7842-0636>  
 Alistair M McInnes: <https://orcid.org/0000-0002-9125-9629>  
 Tegan Carpenter-Kling: <https://orcid.org/0000-0001-8449-2409>  
 Azwianewi B Makhado: <https://orcid.org/0000-0002-1972-264X>

## References

- Adams NJ, Brown CR. 1990. Energetics of molt in penguins. In: Davis LS, Darby JT (eds), *Penguin biology*. San Diego: Academic Press. pp 297–315.
- AEWA. 2020. Benguela Current Forage Fish Workshop 2–4 November 2020. Recommendations. Available at <https://www.unep-awea.org/en/meeting/benguela-current-forage-fish-workshop>
- BirdLife International. 2024. *Spheniscus demersus*. The IUCN Red List of Threatened Species 2024. e.T22697810A256021744. <https://dx.doi.org/10.2305/IUCN.UK.2024-2.RLTS.T22697810A256021744.en> [accessed 8 April 2025].
- Carpenter-Kling T, de Blocq A, Hagen C, Harding C, Morris T, Pichegru L, Roberts J, Ryan PG, Wanless RM, McInnes A. 2022. Important marine areas for endangered African Penguins before and after the crucial stage of moulting. *Scientific Reports* 12: 9489.
- Coetzee JC, de Moor CL. 2024. A summary of the South African sardine fishery. Department of Forestry, Fisheries and the Environment Report: MARAM/IWS/2024/Sardine/BG1. <https://doi.org/10.25375/uct.27908280.v1>
- Cooper J. 1978. Moulting of the black-footed penguin. *International Zoo Yearbook* 18: 22–27. <https://doi.org/10.1111/j.1748-1090.1978.tb00211.x>
- Crawford RJM, Boonstra HGvD, Dyer BM, Upfold L. 1995. Recolonization of Robben Island by African Penguins, 1983–1992. In: Dann P, Norman I, Reilly P. (eds), *The penguins: ecology and management*. Chipping Norton: Surrey Beatty & Sons. pp 333–363.
- Crawford RJM, Shannon LJ, Whittington PA. 1999. Population dynamics of the African Penguin *Spheniscus demersus* at



- Robben Island, South Africa. *Marine Ornithology* 27: 135–143. <https://doi.org/10.5038/2074-1235.27.1.434>
- Crawford RJM, Davis SA, Harding R, Jackson LF, Leshoro TM, Meyer MA, Randall RM, Underhill LG, Upfold L, Van Dalsen AP, Van der Merwe E, Whittington PA, Williams AJ, Wolfaardt AC. 2000. Initial impact of the *Treasure* oil spill on seabirds off western South Africa. *South African Journal of Marine Science* 22: 157–176. <https://doi.org/10.2989/025776100784125645>
- Crawford RJM, David JHM, Shannon LJ, Kemper J, Klages NTW, Roux J-P, Underhill LG, Ward VL, Williams AJ, Wolfaardt AC. 2001. African Penguins as predators and prey – coping (or not) with change. *South African Journal of Marine Science* 23: 435–447. <https://doi.org/10.2989/025776101784528836>
- Crawford RJM, Barham PJ, Underhill LG, Shannon LJ, Coetzee JC, Dyer BM, Leshoro TM, Upfold L. 2006a. The influence of food availability on breeding success of African Penguins *Spheniscus demersus* at Robben Island, South Africa. *Biological Conservation* 132: 119–125. <https://doi.org/10.1016/j.biocon.2006.03.019>
- Crawford RJM, Hemming M, Kemper J, Klages NTW, Randall RM, Underhill LG, Venter AD, Ward VL, Wolfaardt AC. 2006b. Molt of the African Penguin, *Spheniscus demersus*, in relation to its breeding season and food availability. *Acta Zoologica Sinica* 52 (Supplement): 444–447.
- Crawford RJM, Dyer BM, Kemper J, Simmons RE, Upfold L. 2007. Trends in numbers of Cape Cormorants (*Phalacrocorax capensis*) over a 50-year period, 1956–57 to 2006–07. *Emu* 107: 253–261. <https://doi.org/10.1071/MU07015>
- Crawford RJM, Whittington PA, Martin AP, Tree AJ, Makhado AB. 2009. Population trends of seabirds breeding in South Africa's Eastern Cape, and the possible influence of anthropogenic and environmental change. *Marine Ornithology* 37: 159–174. <https://doi.org/10.5038/2074-1235.37.2.831>
- Crawford RJM, Altwegg R, Barham BJ, Barham PJ, Durant JM, Dyer BM, Geldenhuys D, Makhado AB, Pichegru L, Ryan PG, et al. 2011. Collapse of South Africa's penguins in the early 21st century. *African Journal of Marine Science* 33: 139–156. <https://doi.org/10.2989/1814232X.2011.572377>
- Crawford RJM, Makhado AB, Whittington PA, Randall RM, Oosthuizen WH, Waller LJ. 2015. A changing distribution of seabirds in South Africa – the possible impact of climate and its consequences. *Frontiers in Ecology and Evolution* 3: 10. <https://doi.org/10.3389/fevo.2015.00010>
- Crawford RJM, Makhado AB, Oosthuizen WH. 2018. Bottom-up and top-down control of the Benguela ecosystem's seabirds. *Journal of Marine Systems* 188: 133–141. <https://doi.org/10.1016/j.jmarsys.2017.04.004>
- Crawford RJM, Sydeman WJ, Thompson SA, Sherley RB, Makhado AB. 2019. Food habits of an endangered seabird indicate recent poor availability of abundant forage resources. *ICES Journal of Marine Science* 76: 1344–1352.
- Crawford RJM, Sydeman WJ, Tom DB, Thayer JA, Sherley RB, Shannon LJ, McInnes AM, Makhado AB, Hagen C, Furness RW, et al. 2022. Food limitation of seabirds in the Benguela ecosystem and management of their prey base. *Namibian Journal of Environment* 6A: 1–13.
- Cury PM, Boyd IL, Bonhommeau S, Anker-Nilssen T, Crawford RJM, Furness RW, Mills JA, Murphy EJ, Österblom H, Paleczny M, Piatt JF, Roux J-P, Shannon LJ, Sydeman WJ. 2011. Global seabird response to forage fish depletion – one-third for the birds. *Science* 334: 1703–1706. <https://doi.org/10.1126/science.1212928>
- Durbin J, Watson GS. 1950. Testing for serial correlation in least squares regression, I. *Biometrika* 37: 409–428.
- Durbin J, Watson GS. 1951. Testing for serial correlation in least squares regression, II. *Biometrika* 38: 159–178. <https://doi.org/10.1093/biomet/38.1-2.159>
- Gales R, Green B, Stahel C. 1988. The energetics of free-living Little Penguins *Eudyptula minor* (Spheniscidae), during molt. *Australian Journal of Zoology* 36: 159–167. <https://doi.org/10.1071/ZO9880159>
- Hildreth C, Lu JY. 1960. Demand relations with autocorrelated disturbances. *Technical Bulletin, Michigan State University Agricultural Experiment Station, 1960* No. 276, 16 pp.
- Kemper J, Roux J-P, Underhill LG. 2008. Effect of age and breeding status on molt phenology of adult African Penguins (*Spheniscus demersus*) in Namibia. *Auk* 125: 809–819. <https://doi.org/10.1525/auk.2008.06262>
- Kooyman GL, Siniiff DB, Stirling I, Bengtson JL. 2004. Molt habitat, pre- and post-molt diet and post-molt travel of Ross Sea emperor penguins. *Marine Ecology Progress Series* 267: 281–290. <https://doi.org/10.3354/meps267281>
- Leith F, Grigg JL, Barham BJ, Barham PJ, Ludynia K, McGeorge C, Mdluli A, Parsons NJ, Waller LJ, Sherley RB. 2022. Intercolony variation in reproductive skipping in the African penguin. *Ecology and Evolution* 12: e9255. <https://doi.org/10.1002/ece3.9255>
- Ludynia K, Waller LJ, Sherley RB, Abadi F, Galada Y, Geldenhuys D, Crawford RJM, Shannon LJ, Jarre A. 2014. Processes influencing the population dynamics and conservation of African Penguins on Dyer Island, South Africa. *African Journal of Marine Science* 36: 253–267. <https://doi.org/10.2989/1814232X.2014.929027>
- Makhado AB, Tom DB, Dyer BM, Masotla M, Upfold L, Crawford RJM. 2025. Numbers, trends, status, and conservation of African Penguin (*Spheniscus demersus*). In: Makhado AB, Amaro A, Crawford RJM, Gottlieb TR, Morais M, Mwaala DN, Nghimwatya, Seakamela SM, Tom DB, Whittington PA, Witteveen M (eds), *Atlas of marine turtles, seabirds and seals in the Benguela Current and adjacent regions. Population sizes and trends, conservation status and Important Bird and Biodiversity Areas for breeding*. Swakopmund: Benguela Current Convention, and Cape Town: Department of Forestry, Fisheries and the Environment. pp 311–322.
- McInnes AM, McGeorge C, Ginsberg S, Pichegru L, Pistorius PA. 2017. Group foraging increases foraging efficiency in a piscivorous diver, the African Penguin. *Royal Society Open Science* 4: 170918. <https://doi.org/10.1098/rsos.170918>
- McInnes AM, Weideman EA, Carpenter-Kling T, Barham P, Christian M, Day K, Glencross JS, Hagen C, Kock A, Lawrence C, et al. 2024. Commercial fishery no-take zones for African Penguins minimize fisheries losses at the expense of conservation gains. *ICES Journal of Marine Science* 81: 1632–1646. <https://doi.org/10.1093/icesjms/fsae109>
- McInnes AM, Crawford RJM, Makhado AB. 2025. Cape Cormorant *Phalacrocorax capensis*. In: Lee ATK, Rose SJ, Banda S, Bezeng SB, Maphalala MI, Maphisa DH, Smit-Robinson H (eds), *The 2025 Red Data Book of Birds of South Africa, Lesotho and Eswatini*. Johannesburg: BirdLife South Africa. Available at: <https://www.birdlife.org.za/red-list/cape-cormorant/>
- Mdluli A, Barham PJ. 2022. Change in molt behaviour of African Penguins *Spheniscus demersus* on Robben Island. *Biodiversity Observations* 12: 9–14. <https://doi.org/10.15641/bo.1199>
- Morgenthaler A, Frere E, Rey AR, Torlaschi C, Cedrola P, Tiberi E, Mendieta E, Carranza ML, Acardi S, Collm N, et al. 2018. Unusual number of Southern Rockhopper Penguins, *Eudyptes chrysocome*, molting and dying along the Southern Patagonian coast of Argentina: pre-molting dispersion event related to adverse oceanographic conditions? *Polar Biology* 41: 1041–1047. <https://doi.org/10.1007/s00300-018-2264-y>
- Pistorius P. 2025. Cape Gannet *Morus capensis*. In: Lee ATK, Rose SJ, Banda S, Bezeng SB, Maphalala MI, Maphisa DH, Smit-Robinson H (eds), *The 2025 Red Data Book of Birds of South Africa, Lesotho and Eswatini*. Johannesburg: BirdLife South Africa. Available at: <https://www.birdlife.org.za/red-list/cape-gannet/>
- Punt AE, Furness RW, Parma AM, Plagányi-Lloyd E, Sanchirico JN, Trathan P. 2023. Report of the international review panel regarding fishing closures adjacent to South Africa's African Penguin breeding colonies and declines in the

- penguin population. Department of Forestry, Fisheries and the Environment, Cape Town, South Africa. Available at <https://biodiversitylaw.org/wp-content/uploads/2024/03/International-Panel-Report-August-2023.pdf>
- R Core Team. 2025. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Randall RM. 1983. Biology of the jackass penguin *Spheniscus demersus* (L.) at St. Croix Island, South Africa. PhD thesis, University of Port Elizabeth, South Africa.
- Randall RM. 1989. Jackass penguins. In: Payne ALL, Crawford RJM (eds), *Oceans of life off southern Africa*. Cape Town: Vlaeberg Publishers. pp 244–256.
- Randall RM, Randall BM. 1981. The annual cycle of the jackass penguin *Spheniscus demersus* at St. Croix Island, South Africa. In: Cooper J (ed), *Proceedings of the Symposium of birds of the sea & shore*. Cape Town: African Seabird Group. pp 427–450.
- Randall RM, Randall BM, Cooper J, Frost PGH. 1986. A new census method for penguins tested on jackass penguins *Spheniscus demersus*. *Ostrich* 57: 211–215. <https://doi.org/10.1080/00306525.1986.9633658>
- Robinson WML, Butterworth DS, Plaganyi EE. 2015. Quantifying the projected impact of the South African sardine fishery on the Robben Island penguin colony. *ICES Journal of Marine Science* 72: 1822–1833. <https://doi.org/10.1093/icesjms/fsv035>
- Ryan PG, Edwards L, Pichegru L. 2012. African Penguins *Spheniscus demersus*, bait balls and the Allee effect. *Ardea* 100: 89–94. <https://doi.org/10.5253/078.100.0113>
- Saraux C, Sydeman W, Piatt J, Anker-Nilssen T, Hentati-Sundberg J, Bertrand S, Cury P, Furness RW, Mills JA, Österblom H, et al. 2021. Seabird-induced natural mortality of forage fish varies with fish abundance: evidence from five ecosystems. *Fish and Fisheries* 22: 262–279. <https://doi.org/10.1111/faf.12517>
- Shannon LJ, Lockerbie EM, Sparks DA. 2024. *An Ecosystem-level status report for southern Benguela fisheries*. Unpublished report, Amethyst Independent Facilitation.
- Sherley RB, Abadi F, Ludynia K, Barham BJ, Clark AE, Altwegg R. 2014a. Age-specific survival and movement among major African Penguin *Spheniscus demersus* colonies. *Ibis* 156: 716–728. <https://doi.org/10.1111/ibi.12189>
- Sherley RB, Waller LJ, Strauss V, Geldenhuys D, Underhill LG, Parsons NJ. 2014b. Hand-rearing, release and survival of African Penguin chicks abandoned before independence by moulting parents. *PLoS ONE* 9: e110794. <https://doi.org/10.1371/journal.pone.0110794>
- Sherley RB, Crawford RJM, Dyer BM, Kemper J, Makhado AB, Masotla M, Pichegru L, Pistorius PA, Roux J-P, Ryan PG, et al. 2019. The status and conservation of Cape Gannets *Morus capensis*. *Ostrich* 90: 335–346. <https://doi.org/10.2989/00306525.2019.1684396>
- Sherley RB, Makhado AB, Crawford RJM, Hagen C, Kemper J, Ludynia K, Masotla MJ, McInnes A, Pichegru L, Tom D, et al. 2024. The African Penguin *Spheniscus demersus* should be considered Critically Endangered. *Ostrich* 95: 181–187. <https://doi.org/10.2989/00306525.2024.2355618>
- Southwell D, Emmerson L, Forcada J, Southwell C. 2015. A bioenergetics model for estimating prey consumption by an Adélie penguin population in East Antarctica. *Marine Ecology Progress Series* 526: 183–197. <https://doi.org/10.3354/meps11182>
- Underhill LG, Crawford RJM. 1999. Season of moult of African Penguins at Robben Island, South Africa, and its variation, 1988–1998. *South African Journal of Marine Science* 21: 437–441. <https://doi.org/10.2989/025776199784126015>
- Underhill LG, Crawford RJM, Wolfaardt AC, Whittington PA, Dyer BM, Leshoro TM, Ruthenberg M, Upfold L, Visagie J. 2006. Regionally coherent trends in colonies of African Penguins *Spheniscus demersus* in the Western Cape, South Africa, 1987–2005. *African Journal of Marine Science* 28: 697–704. <https://doi.org/10.2989/18142320609504218>
- Weller F, Cecchini L-A, Shannon L, Sherley RB, Crawford RJM, Altwegg R, Scott L, Stewart T, Jarre A. 2014. A system dynamics approach to modelling multiple drivers of the African Penguin population on Robben Island, South Africa. *Ecological Modelling* 277: 38–56. <https://doi.org/10.1016/j.ecolmodel.2014.01.013>
- Whittington PA, Klages NTW, Crawford RJM, Wolfaardt AC, Kemper J. 2005a. Age at first breeding of the African Penguin. *Ostrich* 76: 14–20. <https://doi.org/10.2989/00306520509485468>
- Whittington PA, Randall RM, Randall BM, Wolfaardt AC, Crawford RJM, Klages NTW, Bartlett PA, Chesselet YJ, Jones R. 2005b. Patterns of movements of the African penguin in South Africa and Namibia. *African Journal of Marine Science* 27: 215–229. <https://doi.org/10.2989/18142320509504080>
- Wilson RP. 1985. The Jackass Penguin (*Spheniscus demersus*) as a pelagic predator. *Marine Ecology Progress Series* 25: 219–227. <https://doi.org/10.3354/meps025219>
- Wolfaardt AC, Underhill LG, Crawford RJM. 2009. Comparison of moult phenology of African Penguins *Spheniscus demersus* at Robben and Dassen Islands. *African Journal of Marine Science* 31: 19–29. <https://doi.org/10.2989/AJMS.2009.31.1.2.773>
- Wood SN. 2003. Thin-plate regression splines. *Journal of the Royal Statistical Society (B)* 65: 95–114. <https://doi.org/10.1111/1467-9868.00374>
- Wood SN. 2017. *Generalized Additive Models: an introduction with R (2nd edition)*. Boca Raton: Chapman and Hall/CRC Press. <https://doi.org/10.1201/9781315370279>
- Young DS. 2017. *Handbook of regression methods*. Boca Raton: CRC Press/Taylor & Francis Group.
- Zeileis A, Hothorn T. 2002. Diagnostic checking in regression relationships. *R News* 2: 7–10.