# The conservation status and population decline of the African penguin deconstructed in space and time

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## Abstract

African Penguin *Spheniscus demersus* numbers have declined steadily over three generations, resulting in a loss of nearly 60% since of 1989. The breeding population reached an historic low of ~20,850 pairs in 2019. We use count data and JARA, a generalized Bayesian state-space tool for estimating extinction risk estimates under IUCN Red List Criterion A, to assess the current status of the African penguin population at a global scale. We then deconstruct the overall decline in time and space to identify the regional populations most in need of urgent conservation action. The population in South Africa has declined at a faster annual rate (−5.1%, highest posterior density interval, HPDI: −9.1 to −1.1%) than the population in Namibia, which has remained relatively stable since 1989 (−0.1%, HPDI: −3.7 to +3.6%). And within South Africa, the most rapid rate of change has been seen in the Western Cape colonies to the north of Cape Town, which have declined at nearly 10% per annum over the last 20 years. The large declines in the Western Cape (particularly at Dassen Island and Dyer Island), coupled with slower declines at colonies further east have resulted in the Eastern Cape colonies containing ~50% of the South African penguin population in 2019, as compared to ~27% in 1989. These changes have been coincident with changes in the

abundance and availability of the main prey of the African penguin and eastward displacements of a number of other marine resources in South Africa. Our results highlight the dynamic nature of the decline of the African penguin population in both space and time, and identify clear regions in which urgent conservation action is required.

## Introduction

Seabirds are considered to be the most threatened group of birds in the world [1] and globally their populations may have declined by > 70% since 1950 [2]. Seabirds face a number of threats both on land in their colonies, like invasive alien species and disturbance, and in the oceans, such as bycatch and competition with fisheries [3]. In southern Africa, seven seabird species breed only within the influence of the Benguela upwelling ecosystem, which ranges from southern Angola to Algoa Bay in South Africa. Five of these endemics are listed in a threatened category on the global IUCN Red List (Vulnerable or worse), including the African penguin *Spheniscus demersus* which was first listed as Endangered in 2010 [4].

The African penguin breeds, or has bred, at 32 island and mainland colonies between central Namibia (Hollam's Bird Island) and South Africa's Eastern Cape province (Bird Island; Figure 1; [5]. The breeding colonies are located in three core groups, Namibia, South Africa's Western Cape and South Africa's Eastern Cape, each separated from another by c. 600 km. Although the total population at the turn of the 20$^{th}$ century is not known, it is thought that there may have been as many as 1.5–3.0 million individuals across the species range [6,7]. By 1956, this number was closer to 0.3 million birds, and the population has more or less declined consistently since then apart from a period in the late-1990s and early-2000s when numbers in the Western Cape briefly recovered [4]. This population change since the 1950s has linked to a number of top-down and bottom-up process, including historic egg collecting and guano scraping, changes in the abundance and distribution of their main prey (sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus*), pollution, habitat loss and modification, predation and competition with seals and fisheries, and climate change [8–11].

Arguably the best studied seabird in the region, penguin breeding populations have been counted at all major colonies in South Africa since 1979 and at the four major colonies in Namibia since 1986 [5]. Here, we use these count data and a generalized Bayesian state-space tool for estimating extinction risk estimates under IUCN Red List Criterion A (Just Another Red List Assessment [JARA], [12,13]) to assess the current status of the African penguin population at a global scale. We then deconstruct the overall decline in time and space to identify the regional populations most in need of urgent conservation action. Finally, we review the threats faced by the species and identify interventions needed to secure the species' conservation in light of our findings.

## Methods

### Penguin count data

In South Africa, the numbers of occupied nest sites of African penguins were counted at most extant breeding colonies sporadically between 1979 and 1991 and annually since then [4,14]. We used counts from 18 localities where penguins breed in South Africa for more than 5 of the 41 years from 1979 to 2019 (Figure S1). Of a possible 737 annual counts, 481 were made and 256 were missed. In Namibia, counts were made more or less annually between 1986 and 2016 at the four major colonies that constitute > 95% of the breeding population in that country, Mercury Island, Ichaboe Island, Halifax Island, and Possession Island [15] (Figure S2).

The methods used to count the numbers of occupied nest sites of African penguins have been outlined in detail by [4,14]. Briefly, counts were undertaken by teams of people walking through a penguin colony and counting occupied nest sites. Larger colonies were broken down into predefined census areas, each of which was counted separately. Counts were predominately made between February and September each year [4]. At some small and difficult to access localities counts made outside the main breeding season were used if no other count was available for that year. Where more than one count was made at a locality in a year, the highest count was taken to represent the number of pairs breeding there in that year [4]. An occupied site was considered active if it contained fresh eggs or chicks, or was defended by a non-moulting adult penguin, and considered potential if it was not active but showed recent signs of use, e.g. the presence of substantial quantities of fresh guano or nesting material, the recent excavation of sand from a burrow nest, the presence of many penguin footprints in its vicinity, or a combination of these factors. Breeding by African penguins is not always synchronous [16], so potential nests are counted as they may be occupied by pairs that have recently finished breeding or that are about to breed [4]. Groups of unguarded chicks (crèches) were divided by two to estimate the number of nest sites they represented, with remainders taken to represent an additional site, e.g. crèches of five and six chicks would both be taken to represent three nests [14].

### Generation length

The generation length for African penguins is calculated as:

$$G = \frac{A + 1}{(1 - \phi_A)}$$

(1)

where $A$ is age of first breeding and $\phi_A$ is adult survival [17]. The IUCN Red List guidelines state "where generation length varies under threat ... the more natural, i.e. pre-disturbance, generation length should be used" (IUCN Standards and Petitions Subcommittee 2017). Accordingly we used $\phi_A$ = 0.81 based on penguins flipper banded and resighted at Robben and Dassen Island between 1989 and 1998 in [18] and between 1994/95 and 1998/99 in [19]. African penguins can breed for the first time at between 4 and 6 years of age [20]. Together these values yield generation length estimates of between 9.2 and 11.2 years. The previous assessment of African penguins used G = 10 years [21], thus we retain that value here for the consistency.

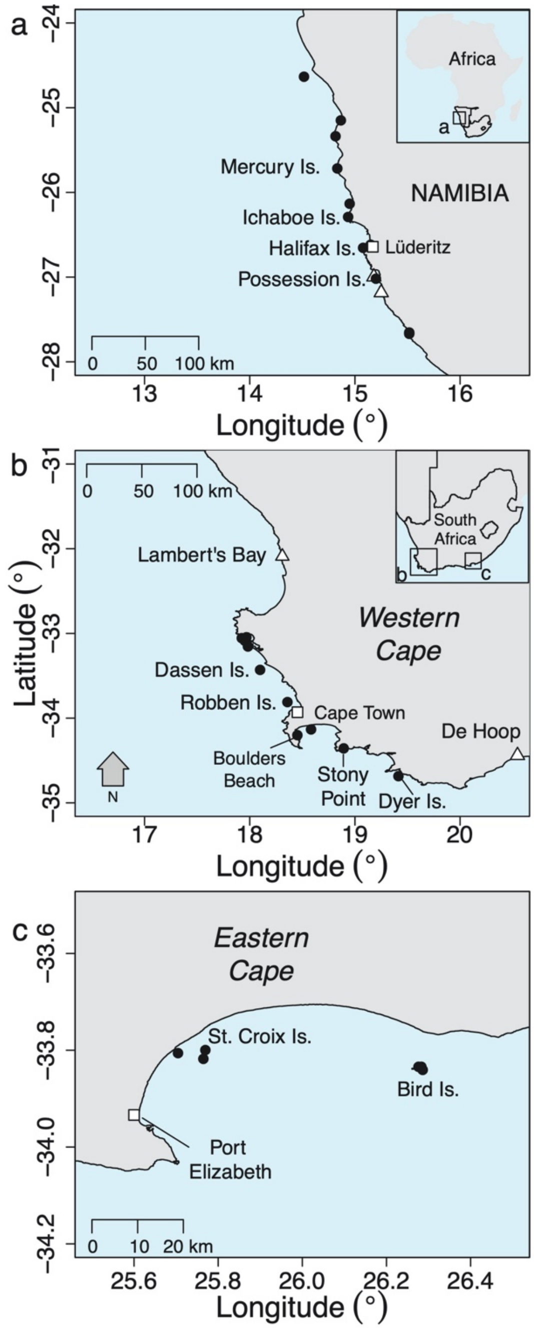


**Figure 1.** The 28 extant (●) and 4 extinct (▲) breeding colonies of the African penguin in South Africa and Namibia. Colonies mentioned in the text are named, as are the major towns and cities (☐) in each region.

**JARA state-space framework**

To determine the trend and rate of change of the African penguin population we used JARA (Just Another Red List Assessment), a generalized Bayesian state-space tool for global extinction risk estimates under IUCN Red List Criterion A [13] that has been applied recently to the Cape gannet *Morus capensis* [22] and several pelagic sharks [12]. JARA assumes that the underlying trend in the population ($I_t$) follows a conventional exponential growth model [23]:

$$I_{t+1} = I_t \lambda_t \tag{2}$$

where $\lambda_t$ is the growth rate in year $t$. On the log scale, the state process model was:

$$\mu_{t+1,i} = \mu_{t,i} + r_{t,i} \tag{3}$$

where $\mu_{t,i} = \log(I_{t,i})$ and $r_{t,i} = \log(\lambda_{t,i})$, the year-to-year rate of change at breeding colony $i$ that is assumed to vary around $\bar{r}_i$ – the underlying mean rate of change for the colony – but with an estimable process variance $\sigma_\eta^2$ that is common to all colonies $r_{t,i} \sim \mathrm{Normal}(\bar{r}_i, \sigma_\eta^2)$. The corresponding observation equation is:

$$\log(y_{t,i}) = \mu_{t,i} + \epsilon_{t,i} \tag{4}$$

where $y_{t,i}$ is the area occupied for year *t* and $\epsilon_{t,i}$ is the observation residual for year $t$ at breeding colony $i$. The residual error is assumed to be normally distributed on the log-scale $\varepsilon_{t,i} \sim \mathrm{Normal}(0, \sigma_\varepsilon^2)$ as a function of a common observation variance $\sigma_\varepsilon^2$. The estimated South African population $\hat{I}_{p,t}$ for year *t* was computed from the sum of all individual colony trajectory posteriors:

$$\hat{I}_{p,t} = \sum_i \exp(\mu_{t,i}) \tag{5}$$

The change (%) in numbers at each colony was calculated from the posteriors of the estimated population trajectory ($\hat{I}_{p,t}$) as the difference between a three-year average around the final observed data point $T$, and a three-year average around year $T - (3\mathrm{G})$. The year $T + 1$ was projected to obtain a three-year average around $T$ to reduce the influence of short-term fluctuations [24].

**Regional variation in conservation status and decline rates**

We first fit JARA simultaneously to the data from all 22 breeding colonies (18 in South Africa and 4 in Namibia) to determine the global trend, conservation status and rates of decline for the African penguin over the last three generation lengths (30 years). Thereafter, we subset the data and refit JARA to (1) the four Namibian colonies only to determine the trend, national status and rates of decline for Namibian; (2) the 18 South African colonies only, to give a perspective on the South African population. Then, to examine regional differences within South Africa, we further subset the data into (3) a West Coast region, in which we considered the seven South African colonies in the Western Cape that are north of Cape Town (Lambert's Bay to Robben Island, Figure 1); (4) a South-West Coast region, which included the five Western Cape colonies south and east of Cape Town (Boulders Beach to Dyer Island, Figure 1); and (5) the six Eastern Cape colonies (Figure 1).

**Bayesian implementation**

We implemented JARA in JAGS (v. 4.3.0) [25] via the 'jagsUI' library (v. 1.5.1) [26] for program R (v. 3.6.1) [27]. The initial for the first modelled count $I_{t=1,i}$ was drawn in log-space from a 'flat' normal distribution with the mean equal to the log of the first observation $y_{t=1,i}$ and a standard deviation of 1000. We used vague normal priors of $\mathrm{Normal}(0,1000)$ for $\bar{r}_i$ and inverse gamma priors for both the state and observation process variance of $\sigma^2 \sim 1/\mathrm{gamma}(0.001,0.001)$, which is approximately uniform on the log scale [28]. We fit all models by running three Monte Carlo Markov chains (MCMC) for 220,000 iterations, with a burn-in of 20,000 and a thinning rate of 4. Convergence was diagnosed using the 'coda' package [29], adopting minimal thresholds of *p* = 0.05 for Heidelberger and Welch [30] and Geweke's diagnostics [31]. Unless otherwise specified, we report medians and 95% highest posterior density intervals (HPDI).

## Results

**Global population**

Over the last 3 generations (30 years), the global African penguin population has declined from ~53,500 pairs to ~20,900 in 2019 (Figure 2a) at a median rate of change of −3.2% (HPDI:−6.9 to +0.7%) per annum (Figure 2b). This corresponds to a 58.8% (78.6–34.5%) decline, with 77.7% probability that the species meets the IUCN Red List classification of globally Endangered (EN) under criterion A2 (Figure 2c). The annual rate of change has remained relatively stable since 1979 (−2.7%, −4.6 to +0.6), but peaked at −4.6% (−4.6 to −0.4%) over the last 2G and then slowing over the last 10 years (1G) to 2.4% (−7.8 to +3.2%) per annum (Figure 2b).

**Namibia – national status and trend**

In Namibia, the African penguin population has remained relatively stable over the last 3G; the modelled population was ~7,000 pairs in 1989 and ~6,300 pairs in 2019 (Figure 3a). The rate of median rate of change varied between −0.1 (−3.7 to +3.6) and 2.0 (−5.3 to +10.0)% (Figure 3b) as the population initially decreased through the 1990s and first half of the 2000s to a low of ~3,600 pairs in 2007, before recovering from 2008 onwards (Figure 3b). Applying the IUCN Red List criterion A2 at a national level in Namibia would yield a classification of Least Concern (LC) with a probability of 80.6% and a median change over 3G of −10.8% (−53.6 to +51.6%), Figure 3c).

**South Africa – national status and trend**

Aside from a period of recovery during the late 1990s and early 2000s, the population in South Africa has decreased more or less consistently since 1979 (Figure 3d), with an annual rate of change of −5.1% (−9.1 to −1.1%) over the last 3G (30 years, Figure 3e). Because of that period of recovery, the rate of change was fastest over the last 2G (20 years) at −7.2% (−11.0 to −3.2%), but the population continued to decline, changing at −5.1% (−10.0 to −0.2%) per annum over the last 1G (10 years, Figure 3e). Applying the IUCN Red List criterion A2 at a national level in South Africa would yield a classification of EN with a probability of 93.9% and a median decline over 3G of 68.6% (82.6 to 54.5%, Figure 3f).

**Regional trends within South Africa**

Within South Africa, the bulk of the recovery seen in the national trend (Figure 3d) resulted from growth in the population in the West Coast region (Figure 4a) mainly Dassen Island and Robben Island (Figure S1). Again, in part because of that period of growth and recovery, the rate decline over the last 2G (20 years) has been substantial, at −9.7% (−15.5 to −3.7%, Figure 4b). However, unlike elsewhere, this rapid decline has persisted in recent years; the rate of change at the colonies in the West Coast region over the last 10 years (1G) was at −9.5% (−16.7 to −2.1%, Figure 4b). Overall, this regional population has declined by 70.2% (77.0– 62.0%) at an annual rate of change of −3.7% (−8.2 to +0.8%) per annum over the last 30 years. Moreover, there is very little uncertainty in this decline; if the IUCN Red List criterion A2 were applied at a regional level, this sub-population would qualify for an EN status with 99.9% probability (Figure S2).

The trend at the South-West Coast region colonies was initially dominated by the continual decline at Dyer Island, from ~23,000 pairs in 1979 to ~2,300 pairs in 1999 and ~1,050 pairs in 2019 (Figure S1); thus the median rate of change since 1979 was −2.2% (−6.3 to +2.3%) overall and 1.0% (−5.6 to +3.5%) since 1989 (3G, Figure 4d). More recently, these decreases at Dyer Island have been offset in this region to a small extent by the colonisation and growth (since the 1980s) of the land-based colonies at Boulders Beach and Stony Point to ~950 and ~1,700 pairs respectively (Figure S1). As these two colonies have come to dominate the population numbers in this region, so the annual rate of change has shifted from negative to positive, ending at +2.7% (−4.6 to +10.0%) in the last 1G (Figure 4d). However, these increases did not offset the ~90% decline of the population at Dyer Island (Figure 4c).

Finally, in the Eastern Cape, the population has decreased fairly consistently since 1989 (Figure 4e) at rate of change ranging from −3.7 (−13.8 to +6.8) to −4.7 (−11.6 to +2.1)% which has in general been slightly slower than the overall rate of change in South Africa (cf. Figure 4f with Figure 3e). Nevertheless, this sub-population has declined by 67.0% (89.1–36.2%) over the last 3G (Figure S2), and has come to represent a far greater proportion of the overall African penguin population in South Africa as a result of the substantial declines at Dyer Island and the colonies north of Cape Town (but in particular Dassen Island. In 1979 the six Eastern Cape colonies contained ~27% of the African penguin population in South Africa. In 2019, they contained ~50%.

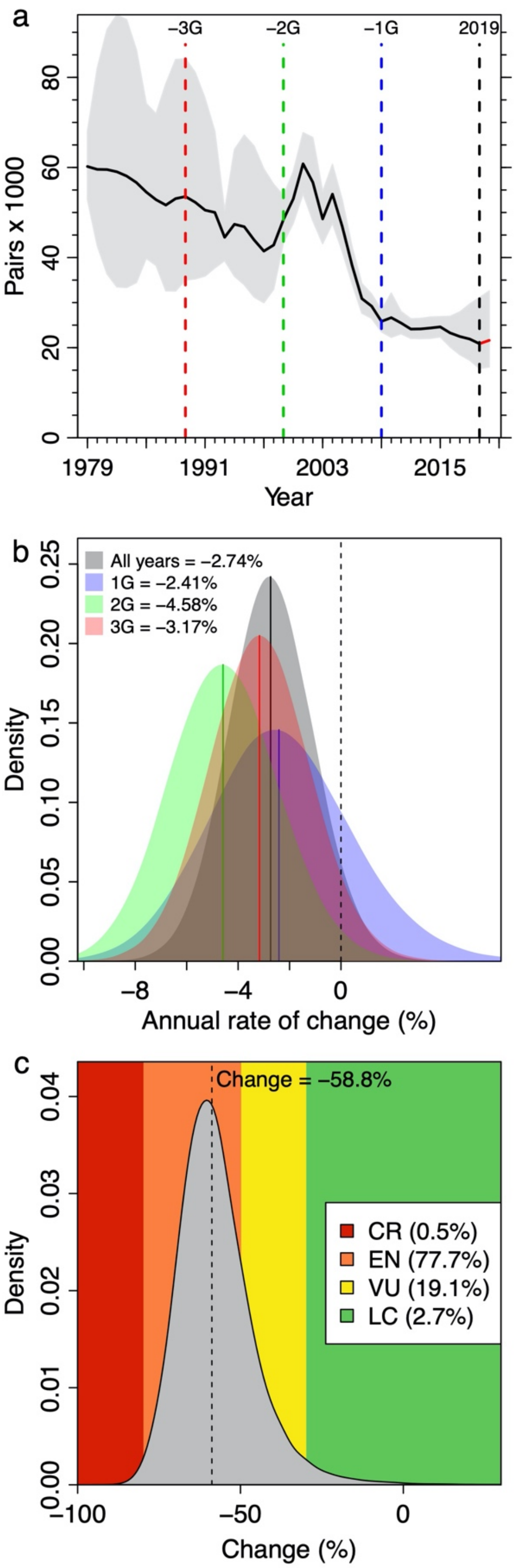


**Figure 2.** The decline in the global African penguin breeding population since 1979. (a) The JARA fitted median (black line) and 95% highest posterior density intervals (HPDI; grey polygon) for the population trend of African penguins in South Africa and Namibia based on nest counts from 22 colonies made between 1979 and 2019. The 10-year generation lengths before 2019 are denoted by a blue dashed line (−1G, 2009), a green dashed line (−2G, 1999) and a red dashed line (−3G, 1989). (b) The posterior medians (solid lines) and probability distributions (coloured polygons) for the annual rate of population change (%) calculated from all the data (1979 to 2019, All years, in black), from the last one generations (1G; in blue), from the last two generations (2G; in green), and the last three generations (3G; in red) shown relative to a stable population (% change = 0, black dashed line). (c) The median change (%, dashed line) in the breeding population of penguins in South Africa over three generations (3G) and corresponding posterior probability (grey polygon) for that change, overlaid on the IUCN Red List category thresholds for the Red List criteria A2. The legend gives the percentage of the posterior probability distribution falling within each Red List category (LC—dark green, VU—yellow, EN—orange, CR—red).

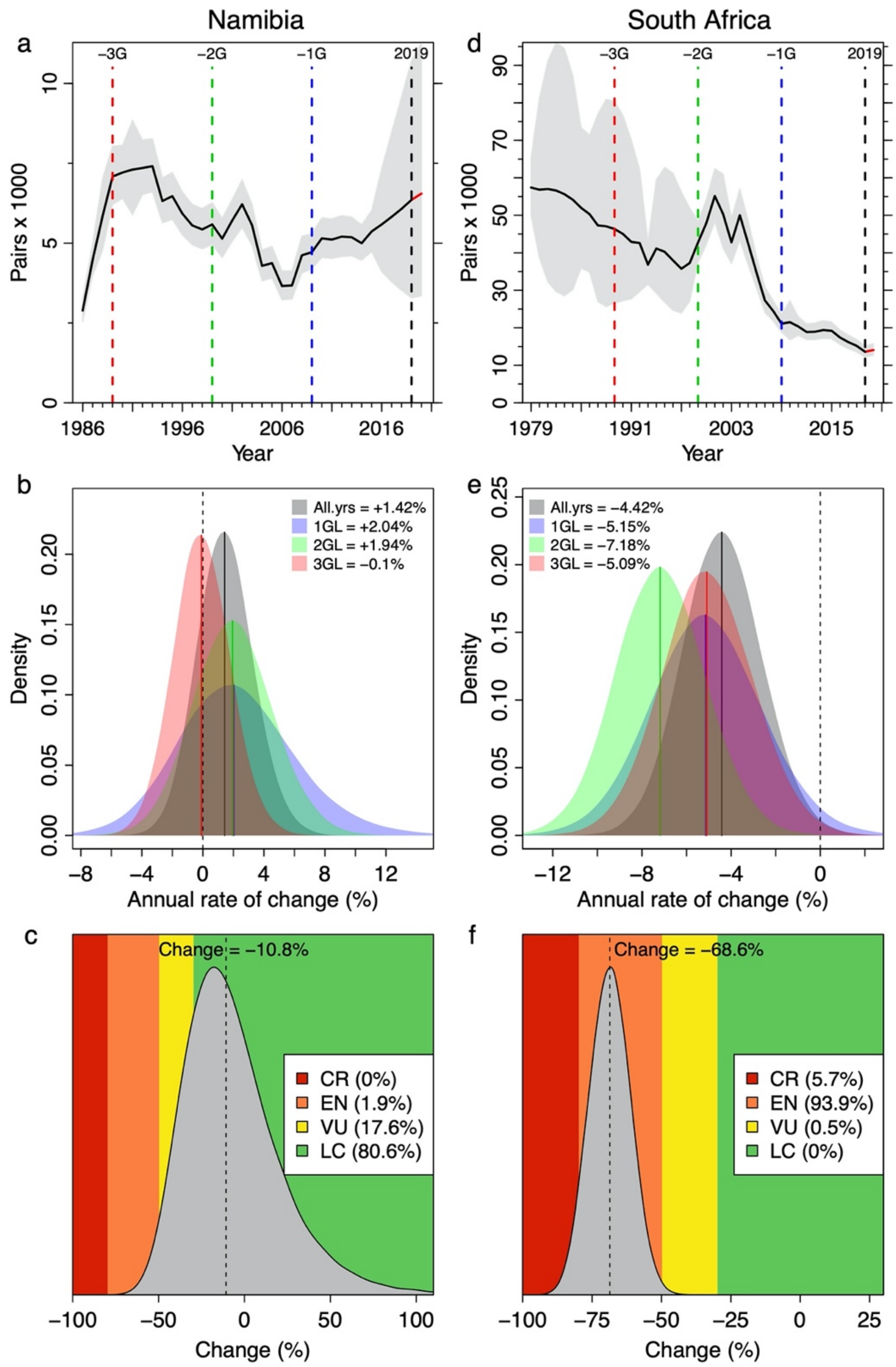


**Figure 3.** The change in the African penguin breeding population in Namibia since 1986 (left) and in South Africa since 1979 (right). (a and d) The median (black line) and 95% HPD (grey polygon) for the national population trends of African penguins. The 10-year generation lengths before 2019 are denoted by a blue dashed line (−1G, 2009), a green dashed line (−2G, 1999) and a red dashed line (−3G, 1989). (b and e) The posterior medians (solid lines) and probability distributions (coloured polygons) for the annual rate of population change (%) calculated from all the data (1979 to 2019, All years, in black), from the last one generations (1G; in blue), from the last two generations (2G; in green), and the last three generations (3G; in red) shown relative to a stable population (% change = 0, black dashed line). (c and f) The

median change (%, dashed line) in the breeding population of penguins in South Africa over three generations (3G) and corresponding posterior probability (grey polygon) for that change, overlaid on the IUCN Red List category thresholds for the Red List criteria A2 (LC—dark green, VU—yellow, EN—orange, CR—red).

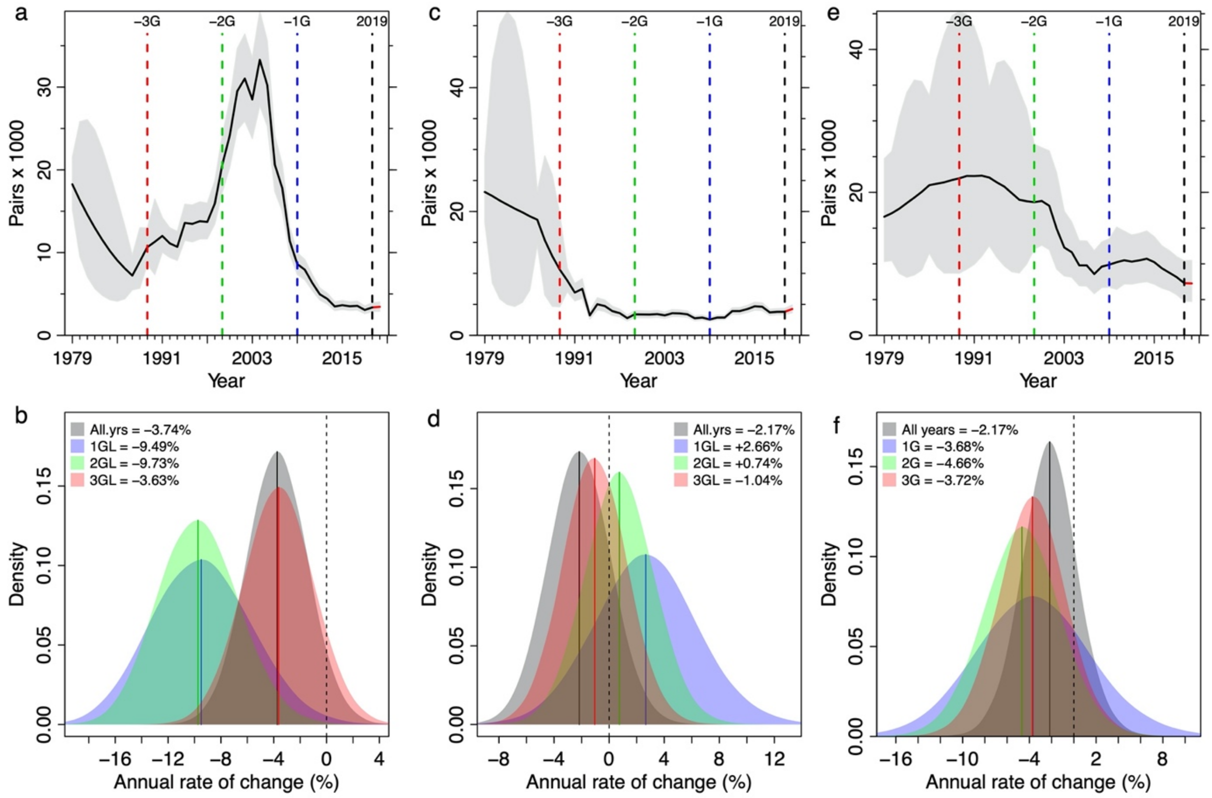


**Figure 4.** The change in the African penguin breeding population within the three regions of South Africa, the West Coast region (Western Cape colonies north of Cape Town; left, a and b), the South-West Coast region (Western Cape colonies south and east of Cape Town, middle, c and d) and the Eastern Cape (right, e and f). (a, c and e) The median (black line) and 95% HPD (grey polygon) for the regional population trends of African penguins. The 10-year generation lengths before 2019 are denoted by a blue dashed line (−1G, 2009), a green dashed line (−2G, 1999) and a red dashed line (−3G, 1989). (b, d and f) The posterior medians (solid lines) and probability distributions (coloured polygons) for the annual rate of population change (%) calculated from all the data (1979 to 2019, All years, in black), from the last one generations (1G; in blue), from the last two generations (2G; in green), and the last three generations (3G; in red) shown relative to a stable population (% change = 0, black dashed line).

## Discussion

African penguin numbers have declined steadily over three generations, resulting in a loss of nearly 60% since of 1989, and reached an historic low of ~20,850 pairs in 2019. Our results show that its classification as Endangered as per the IUCN Red List is warranted going forward. This is clear cause for concern for this species. However, African penguins have not declined at the same rate across their range, which is disjunct between Namibia and the Western and Eastern Cape provinces of South Africa. This is for various reasons, including differences in the nature and severity of threats and local population dynamics. It follows, then, that there are different conservation management priorities for each subpopulation.

The Namibian population has declined slightly over the last three generations, but the rate of decline is insufficient to warrant any Red List classification under the A criterion other than Least Concern. However, the Namibian penguin population had already declined by ~70% prior to the start of our dataset in 1986, coincident with the collapse of the sardine stocks there in the 1970s [8]. This broad scale assessment also masks a worrying decline to 3,600 pairs in 2007 before the subsequent recovery. The low numbers of penguins in Namibia is likely maintained by a scarcity of small pelagic fish [32,33] and the birds' reliance on lower energy prey [34]. Monitoring of breeding colonies in Namibia is an ongoing priority, with an annual census of breeding pairs the minimum requirement to track trends in this population. A recent outbreak of avian influenza in some colonies in Namibia have shown the vulnerability of this population to stochastic events, the effects of which are exacerbated at low population levels [35]. A lack of reliable recent population data curbs the ability of conservation managers to respond to emergent threats and to do assessments.

The South African population has declined at a much faster rate than the one in Namibia, resulting in a national classification of Endangered and driving the global conservation status. Despite a small population recovery in the late 1990s and first half of the 2000s, driven mostly by increases in the West Coast region, there has subsequently been a crash the mid-2000s onwards to an historical low of ~13,500 pairs in 2019. The short-lived population recovery and subsequent crash were associated with a concomitant boom and then decline in sardine and anchovy biomass [36]. The decline also coincided with an eastward displacement in spawning adults of both these fish [37,38] driven by a combination of environmental change and fishing pressure [38,39], which in turn appears to have worsened the availability of prey for seabirds breeding to the north of Cape Town [40]. The South-West Coast region has remained relatively stable at low levels over the last three generations, while the Eastern Cape region has experienced periods of relative stability followed by declines in the early 2000s and the late 2010s. Because the Eastern Cape population has declined at a slower rate than elsewhere in South Africa, the area has become increasingly important in terms of its relative contribution to the national population.

A lack of available food, predominantly small pelagic fish, is believed to be the main driver for declines in South Africa over the last three generations [11,36,40,41], with sporadic oiling events, habitat destruction, disturbance, and predation also contributing to declines [42–45]. Thus, a key intervention is the identification and protection of key foraging areas. This has been initiated through a 10-year experiment to investigate the effects of fishing closures around penguin breeding colonies, which has shown some benefits to breeding penguins through a decrease in foraging effort and an increase in chick growth and condition [46–48], although this has been contested [49–51]. The initial identification of areas used by penguins during other parts of their life cycle such as pre- and post-moult and during the first few years after fledging has begun [11,52] but further work is required to determine the most appropriate mechanism to protect penguins during these vulnerable periods [11]. Additional spatial management of sardine and anchovy fishing effort, currently concentrated on the West Coast, will assist with addressing the mismatch between fish distribution and fishing effort [38,53]. The hand-rearing and release of chicks [54], and the creation of new breeding colonies have also been suggested as additional ways to mitigate the mismatch between penguin breeding colonies and fish distribution [55] and a pilot site is currently being attempted on the southern coast of South Africa.

In 2013, the South African government put in place a Biodiversity Management Plan for the African penguin [55]. This plan aimed to halt the decline of the species and thereafter achieve a population growth rate that would result in the down listing of the species' conservation status. While the plan did not achieve its aim, it provides a more coordinated approach to penguin conservation and many key interventions were initiated through the plan. A revised plan is being prepared with fewer, more threatfocused actions, and will be implemented from 2020. Our results highlight a rapid, unsustainable decline of almost 10% per year at colonies in the geographic core of the species breeding range (the colonies to the north of Cape Town) and denote a shift to a situation in which colonies at the geographic edge of the species range in the Eastern Cape currently form the stronghold of the African penguin population. Algoa Bay (the location of the Eastern Cape penguin colonies) has been identified as a marine transport hub and potentially as an Aquaculture Development Zone, increasing the risks of oil spills and human disturbance and impact on the ecosystem of the bay. Accordingly, the Eastern Cape colonies should be viewed as a priority for conservation interventions, as should actions that could contribute to retaining viable breeding populations at the formally large colonies in the West Coast region.

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# Supplementary Materials

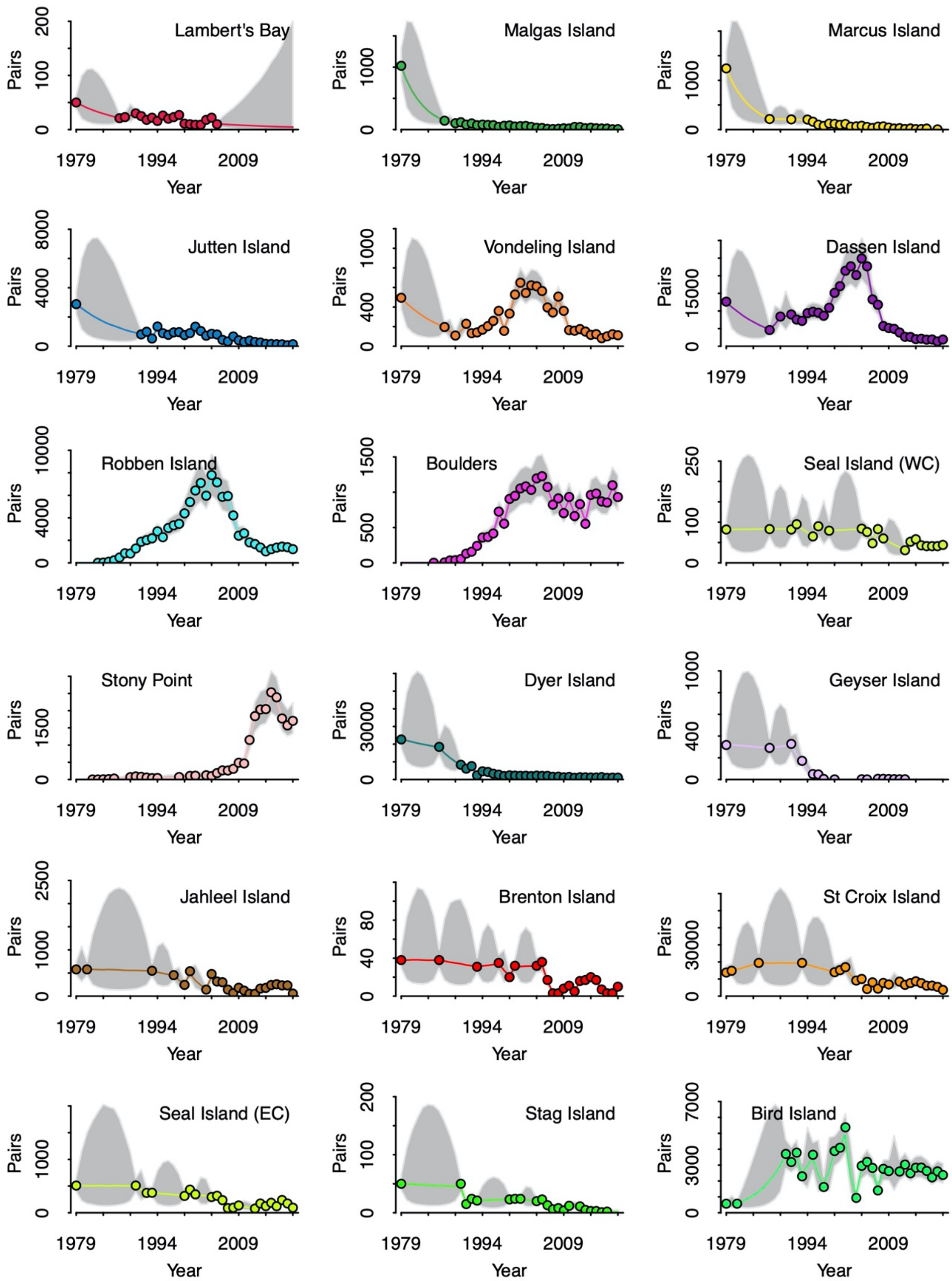


**Figure S1.** Bayesian state-space model fits (lines) from Just Another Red List Assessment (JARA) to population counts (points) made between 1979 and 2019 at 18 of the 19 known colonies in South Africa at which African penguins have bred for more than 5 years during that time frame.

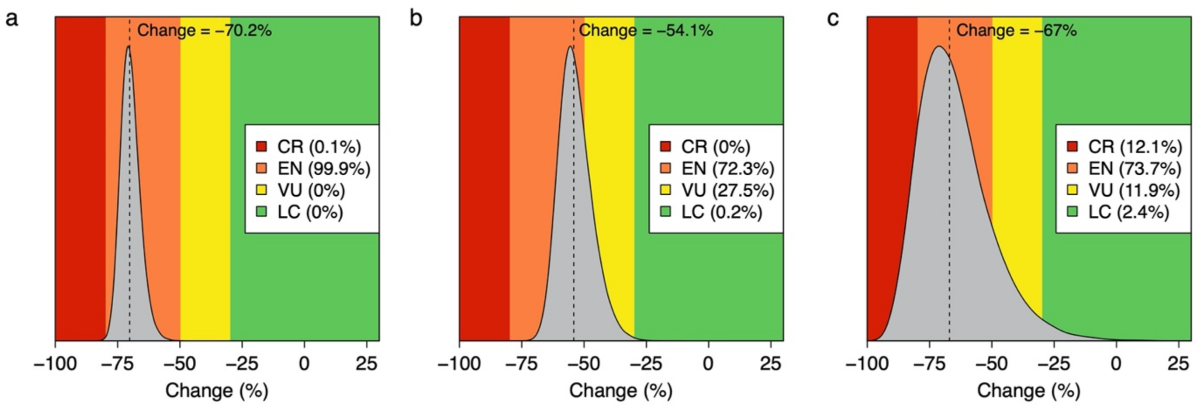


**Figure S2.** The median change (%, dashed line) in the breeding population of penguins in (a) the West Coast region of South Africa, (b) the South-West Coast region of South Africa, and (c) the Eastern Cape province of South Africa over three generations (3G) and corresponding posterior probability (grey polygon) for that change, overlaid on the IUCN Red List category thresholds for the Red List criteria A2 (LC—dark green, VU—yellow, EN—orange, CR—red).