Reproductive skipping behaviour in the African penguin (Spheniscus demersus)

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Abstract

In long-lived species, reproductive skipping is a common strategy whereby sexually mature animals skip a breeding season, potentially reducing population growth. This may be an adaptive decision to protect survival, or a non-adaptive decision driven by individual-specific constraints. Understanding the presence and drivers of this behaviour is key to effective population management, yet in many species such as the endangered African penguin (Spheniscus demersus), these factors remain unknown. This study uses multistate mark-recapture methods to estimate African penguin survival and breeding probabilities at two colonies between 2013 and 2020. Overall, survival was higher at Stony Point (0.82) than Robben Island (0.77). Inter-colony differences were linked to food availability; under decreasing sardine (Sardinops sagax) abundance, survival decreased at Robben Island and increased at Stony Point. Additionally, reproductive skipping was evident across both colonies; at Robben Island ~22% of breeding individuals skipped reproduction each year, versus ~10% at Stony Point. Penguins skipping reproduction had a lower probability of future breeding than breeding individuals; this lack of adaptive benefit suggests reproductive skipping is driven by individual-specific constraints. Lower survival and breeding propensity at Robben Island places this colony in greater need of conservation action. However, further research on the drivers of inter-colony differences is needed.

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Abstract

In long-lived species, reproductive skipping is a common strategy whereby sexually mature animals skip a breeding season, potentially reducing population growth. This may be an adaptive decision to protect survival, or a non-adaptive decision driven by individual-specific constraints. Understanding the presence and drivers of this behaviour is key to effective population management, yet in many species such as the endangered African penguin (*Spheniscus demersus*), these factors remain unknown. This study uses multistate mark-recapture methods to estimate African penguin survival and breeding probabilities at two colonies between 2013 and 2020. Overall, survival was higher at Stony Point (0.82) than Robben Island (0.77). Inter-colony differences were linked to food availability; under decreasing sardine (*Sardinops sagax*) abundance, survival decreased at Robben Island and increased at Stony Point. Additionally, reproductive skipping was evident across both colonies; at Robben Island ~22% of breeding individuals skipped reproduction each year, versus ~10% at Stony Point. Penguins skipping reproduction had a lower probability of future breeding than breeding individuals; this lack of adaptive benefit suggests reproductive skipping is driven by individual-specific constraints. Lower survival and breeding propensity at Robben Island places this colony in greater need of conservation action. However, further research on the drivers of inter-colony differences is needed.

Keywords: *Benguela ecosystem, breeding propensity, mark-recapture, population dynamics, seabirds, survival.*

1. Introduction

Survival and reproduction are two key demographic processes for all organisms, yet both are energetically costly and are in competition for the same limited resources (Williams 1966; Stearns 1992). High investment in reproduction one year diverts energy away from other processes, potentially reducing future survival probabilities and, particularly in long-lived species, impacting on an individual's lifetime reproductive output (Williams 1966). Long-lived species therefore more often act as 'prudent parents', prioritising their own survival over reproduction (Sæther *et al.* 1993; Cam *et al.*1998). This strategy is widespread among long-lived seabirds (Bleu*et al.* 2016), especially among pelagic foragers (e.g., albatrosses; Jouventin & Dobson 2002 and king penguins*Aptenodytes patagonicus* ; Le Bohec *et al.* 2007), which regularly undertake long and energetically costly foraging trips. However, these nonbreeders are often not accounted for in population studies, despite their ability to obscure low population growth rates and reduce the reliability of population estimates (Lee *et al.*2017).

The drivers of reproductive skipping are predominantly grouped into adaptive and non-adaptive explanations. Adaptive explanations suggest animals actively avoid reproduction when conditions are poor (e.g., low food availability; Gauthier-Clerc *et al.* 2001) to enhance survival, ensure future breeding opportunities and improve lifetime reproductive output. Alternatively, reproductive skipping may be driven by non-adaptive individual constraints. For example, unavoidable events like pair-bond breakdown or forced nest site relocation may occur (Bradley *et al.* 2000; Jeschke *et al.* 2007; Salas *et al.* 2020)**.** Additionally, the intrinsic quality of animals will vary regardless of these mechanisms, with some 'higher quality' individuals consistently achieving higher

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survival and reproductive rates (Cam *et al.* 1998; Jenouvrier *et al.* 2015). In reality these mechanisms co-occur. For example, 'lower quality' individuals are more likely than 'high quality' individuals to adaptively skip reproduction under poor conditions (Robert *et al.*2012; Souchay *et al.* 2018). The extent and drivers of reproductive skipping therefore vary not only between species and populations, but also at the individual level. Characterising inter-population variation in reproductive skipping is therefore vital to understand better localised population dynamics and to identify areas in need of conservation action. However, in many species reproductive skipping is yet to be evaluated; the endangered African penguin (*Spheniscus demersus*) is a key example of this, and the focus of our study.

The African penguin is endemic to South Africa and Namibia, feeding on sardine (*Sardinops sagax*) and anchovy (*Engraulis encrasicolus*) stocks in the Benguela upwelling system (Wilson 1985). Since 1989, the African penguin population has declined by almost 65%, with the fastest declines occurring at colonies in South Africa's Western Cape (Sherley *et al.* 2020). While historically driven by egg collection and guano scraping (Frost *et al.* 1976; Crawford*et al.* 2018), current declines are predominantly attributed to reduced prey availability (Crawford *et al.* 2011; Sherley *et al.* 2020). Shifting geographic distributions of sardine and anchovy, the main prey of African penguins, apparently exacerbated by competition with fisheries, have been linked to both reduced survival (Sherley*et al.* 2014, Robinson et al. 2015) and lower breeding success (Crawford *et al.* 2006; Sherley *et al.* 2013, 2021). However, population growth is strongly influenced not only by survival and breeding success, but also the proportion of the population that breeds each year (Cam *et al.* 1998; Le Bohec *et al.* 2007). Characterising the presence and drivers of reproductive skipping is therefore fundamental to improve our understanding of African penguin population dynamics to guide future protection of this endangered species.

Here we use mark-recapture data from two African penguin colonies in the Western Cape, spanning an 8-year period (2013–2020). Changes in survival and breeding propensity were examined over time and between colonies, with a focus on understanding the presence and trends in reproductive skipping behaviour. The effects of food availability on survival and breeding propensity were also examined, in line with previous work linking food availability to changes in survival and breeding success in this species (e.g., Crawford *et al.* 2011).

2. Materials and Methods

2.1 Study site and data collection

Data collection took place between 2013 and 2020 at two African penguin colonies in the Western Cape Province, South Africa: Robben Island (33°48' S, 18°22' E) and Stony Point (34@22'S, 18@53'E) (Figure 1). From 2013 onwards, penguins were captured in each colony, and injected with passive integrated transponders (PITs). For 2013 and 2014 these were Half Duplex (HDX), 134.2 kHz, ISO 11784/11785 compliant, 32mm glass PITs (31.2 [l] × 3.85 [d] mm, weight 0.8 g), injected subcutaneously into the back of the neck. From 2015, Full Duplex (FDX-B), 134.2 KHz, ISO compliant, 12 mm PITs (Biomark, Boise ID, USA) were injected subcutaneously into the skin flap posterior to the left leg. Subsequent encounter data of tagged penguins were then collected from 2014 onwards. As part of routine nest monitoring between March and October, the presence and breeding status (breeding or nonbreeding) of tagged birds was identified using a hand-held transponder reader (Datamars model GES3SEU with external stick antenna from 2014–2015, Allflex model RS420 from 2016 onwards). Each year captured untagged birds were tagged under the same protocol (Table A1, Appendix). Supplementing this, ground reader systems (Biomark IS1001 with loop antenna) were installed across commonly used highways to/from the sea; one reader was installed at Robben Island in 2015, and two at Stony Point in 2016 and 2017 respectively. Although not completely curtailed in either season, data collection using the hand-held transponder readers was negatively impacted by an Avian Influenza outbreak in 2018 (Molini *et al* . 2020), which limited close approaches by researchers to penguin nests, and by the COVID-19 pandemic in 2020, which limited the number of person-days spent in the field (relative to other breeding seasons), particularly at Robben Island.

2.2 Encounter data

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We used mark-recapture data from 899 adult penguins, 387 at Robben Island and 512 at Stony Point (Table A1). Encounter data were collected over the breeding season (March to October); survival rates consequently refer to the nonbreeding season (November to February). We assigned each penguin a state both during initial marking and each subsequent encounter. Individuals were considered breeders if they were attending chicks or eggs in a nest site or guarding a nest site during nest inspections. Additionally, if they were encountered in the colony via the ground reader [?] 6 times over a minimum of 12 days and a maximum of 120 days but not confirmed as breeders during nest inspections, they were considered breeders based on knowledge of African penguin breeding biology (Williams & Cooper 1984). To ensure that any birds encountered as nonbreeders were definitely skipping reproduction and were not younger birds yet to breed for the first time, we included an additional state of 'prebreeder', assigned to any birds marked/encountered as nonbreeders that had not yet been encountered breeding within their encounter histories.

Earlier tagging of African penguins used stainless steel flipper bands (e.g., Sherley *et al.* 2014). However, these have now been phased out due to potential data bias, both through human error (e.g., incorrectly reading tags) and potential deleterious effects on penguin survival and behaviour (e.g., Dugger *et al.* 2006; Dann *et al.* 2014). Within this dataset, four double marked (flipper band from previous tagging, and transponder from this study) individuals were removed to reduce any potential bias. Additionally, movement between colonies is rare in breeding African penguins (Sherley *et al.*2014); here, one individual encountered breeding at >1 colony was removed from the dataset to improve the reliability of model estimates by reducing the need for more complex models incorporating inter-colony movement (as this was not the focus of our study).

2.3 Fish biomass data

To determine the impact of food availability on survival and breeding probabilities in African penguins, we used estimates of sardine and anchovy spawner (fish aged [?]1 year) biomass from hydro-acoustic surveys conducted by the Department of Forestry, Fisheries, and the Environment (DFFE) in November each year between 2013 and 2019 (Coetzee & Merkle 2019, Coetzee *et al* . 2020). For detailed survey methods see Coetzee *et al.* (2008). We considered the portion of the biomass estimated to occur West of Cape Agulhas (WoCA), as prey availability in this region has previously been linked to measures of penguin survival and reproduction (e.g., Sherley *et al* . 2013, Robinson *et al* . 2015). Because the spawner biomass survey occurs during the penguins' nonbreeding season, we related the biomass WoCA to survival using the biomass from the survey at the start of the nonbreeding period (i.e., for survival from 2013 to 2014, the WoCA estimate for November 2013 was used), and considered the biomass of the two species (sardine and anchovy) combined and for each separately in our modelling framework.

2.4 Multistate mark-recapture models

To estimate the probabilities of survival (Φ), encounter (or recapture, ρ) , and transition (ψ) between states (breeder, non-breeder, and prebreeder), multistate mark-recapture models were constructed using program MARK and the 'RMark' package in R (White & Burnham 1999; Laake 2013). Within these models, a group effect for colony (Robben Island and Stony Point) was included to evaluate colony differences in the estimates. Known parameters were fixed to improve model performance; since only breeders were marked in 2013 across both colonies (with nonbreeders marked in subsequent years, Table A1), survival and transition rates for nonbreeders and prebreeders were fixed to zero during 2013–14, as was recapture in 2014 in both colonies. Additionally, no nonbreeders were marked in 2014 at Robben Island, so prebreeder survival and transition during 2014–15, and prebreeder recapture in 2015 were also fixed to zero for this colony.

Initially, a general model was developed assuming time, state, and colony dependence for survival, recapture, and transition probabilities. Simpler model structures were also tested for recapture whereby years were pooled into two groups to represent before and after ground readers were installed in each colony. For survival and transition, simpler models were also included whereby time dependence was replaced with both combined and separated annual sardine and anchovy spawner biomass WoCA to determine whether fish abundance offered better predictive power for survival and transition probabilities than the fully time-

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dependent model.

Recapture probabilities were modelled first, with the best fitting model taken forward to assess survival probabilities, followed by transition. Model selection was based on Akaike's Information Criterion corrected for over-dispersion and small sample size (QAICc) (Lebreton *et al.* 1992). When models differed by QAICc <2, they were considered approximately equivalent (Burnham & Anderson 2002), and the model with the lowest number of parameters was considered the most parsimonious. Goodness-of-fit (GOF) tests for the general model (JMV model; Pradel *et al.* 2003) were performed using package 'R2ucare' (Gimenez *et al.* 2018) in Program R.

3. Results

The overall GOF test for the general (JMV) model showed significant lack of fit to the data ($\chi^2_{65} = 115.62$, p < 0.001, detailed results in Table A2 in the Appendix). This lack of fit was accounted for during model selection using a variance inflation factor ($\hat{c} = 1.78$).

3.1 Encounter

The best supported model for encounter (model A10, Table A3 in the Appendix) included an interactive effect of time and colony (Robben Island and Stony Point), and an additive effect of state (breeder, nonbreeder, and prebreeder). At Stony point, encounter rates appeared lower during 2015 and 2016, increasing up to 2018 and 2019, followed by a decrease in nonbreeder and prebreeder encounter in 2020 (Figure 2). Meanwhile at Robben Island, a general increase in encounter probability for nonbreeders and prebreeders was evident between 2015 and 2018, followed by a decrease, while breeder encounter rates remained consistently high (Figure 2). Regardless of colony, the probability of encountering breeders was consistently higher than nonbreeders and prebreeders, with all estimable breeder encounter estimates >0.9 at Robben, and 4 out of 6 estimates >0.9 at Stony Point.

3.2 Survival

The probability of survival was variable at both colonies, ranging from 0.62 to 0.89 at Stony Point, and 0.65 to 0.87 at Robben Island. Overall survival (± SE) was slightly higher at Stony Point (0.82 ± 0.01) than Robben Island (0.77 ± 0.02) based on a constant model. However, the best supported survival model (model B22, Table A3 in the appendix) contained an interaction between sardine spawner biomass WoCA and colony; the relationship was positive at Robben Island, but negative at Stony Point (Figure 3). There was some support for an interaction between time and colony (model B32, Table A3 in the appendix), but this model produced a higher QAICc and contained more parameters, and so was not retained as the best model. Some support was shown for an additive effect of state on survival (model B24, Table A3 in the appendix), with breeding individuals exhibiting slightly higher survival rates, but this was not retained in the best model.

3.3 Transition

Strong support for a three-way interaction between time, colony and state on transition probabilities was evident from the model selection (model C36, Table A3 in the appendix). At both colonies, breeding individuals were more likely to breed again than to skip reproduction the following year except in 2019/20 at Robben Island (Figure 4a). However, breeding individuals were generally more likely to skip reproduction at Robben Island than at Stony Point. Individuals at Robben Island also showed an increasing prevalence for reproductive skipping from 2014 onwards (Figure 4a). Colony differences were especially evident between 2017/18 and 2019/20, with all estimates at Robben Island >0.3, whereas estimates at Stony Point were all <0.1 (Figure 4a).

Transitions out of the nonbreeding state were more variable and less accurately estimated (Figure 4b). At Robben Island, the probability of nonbreeding birds becoming breeders increased between 2015/16 and 2018/19, followed by a decrease in 2019/20, but estimates at Stony Point showed no clear trend. Overall, nonbreeders were more likely to breed the following year than skip reproduction again (overall probability

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± SE = 0.66 ± 0.06 at Robben Island and 0.69 ± 0.06 at Stony Point, based on a constant model). However, individuals skipping reproduction were still generally less likely to breed the next year than breeding individuals (Figure 4).

Finally, transition estimates for prebreeders were also poorly estimated, because of the small number of individuals in this state, especially during the earlier years of the study. However, the estimates suggest a general decrease in the probability of transitioning into a breeding state over time at both colonies, but with prebreeders consistently more likely to breed the following year at Stony Point than at Robben Island (Figure 4c).

4. Discussion

Reproduction and survival are key demographic parameters impacting population dynamics (Stearns 1992). We used mark-recapture techniques to evaluate these parameters for the African penguin at two colonies and confirmed the presence of reproductive skipping behaviour. We illustrate that variation in survival is driven by food availability, with lower sardine abundance linked to lower survival at Robben Island, and higher survival at Stony Point. Similarly inter-colony differences were evident in breeding propensity; reproductive skipping occurred at both colonies, but at a higher rate at Robben Island than at Stony Point. Alongside providing key demographic information on the endangered African penguin, this study represents the first reliable estimates of reproductive skipping in this species.

4.1 Survival

Adult survival of seabirds is generally high (Dias *et al.* 2019). Long-term mean adult survival rates for penguins usually exceed 0.8, with most (9 of 13 species reported) above 0.85 (Bird *et al.* 2020). Even in a population of Magellanic penguins (*S. magellanicus*), declining at ~1.3% per annum, adult survival was >0.8 in 23 of 25 study years (92%; Gownaris & Boersma 2019). Based on this, African penguin survival rates in this study appear to be relatively low compared to other penguin species, especially at Robben Island (0.77 ± 0.02) where survival was only >0.8 in 2 of 7 years (28%). However, our estimates remain consistent with previous estimates for African penguins (e.g., Wolfaardt *et al.* , 2008; Sherley *et al.* , 2014) and represent the first survival estimates from African penguins where no individuals were tagged with potentially harmful flipper bands. Within this study, we found that changes in survival are predominantly driven by changing prey (sardine) abundance, with lower abundance underpinning lower survival at Robben Island and higher survival at Stony Point. Understanding the drivers of these colony-specific differences is fundamental to successful future population management of African penguins.

The finding that survival declines along with sardine abundance at Robben Island is consistent with previous literature (Sherley *et al.* 2014; Robinson *et al.* 2015). This response underlines the recent concern for the long-term viability of the colony at Robben Island (e.g. Sherley *et al* . 2018), given the low and declining availability of sardine to seabirds off western South Africa (Robinson *et al.* 2015, Crawford *et al* . 2019). However, the increasing survival rates with decreasing food abundance in individuals at Stony Point are more surprising. This may be explained by the presence of additional factors (e.g., predation, density dependence) which can impact survival differently across colonies (Weller *et al* . 2016); i.e., food availability may not currently be the dominant external driver of variation in survival at Stony Point. Alternatively, this may be explained by limitations within our analysis; for example, the fisheries data we used index fish abundance across a large area of South Africa's coastal waters (Coetzee *et al.* 2008) and may not necessarily adequately reflect localised food availability at both colonies. Eastward displacement of sardine and anchovy in the Benguela upwelling system is driving decreased food availability for seabirds in the Western Cape (Crawford 2007, Crawford *et al* . 2019). With Stony Point located >70km south-east of Robben Island, localised food availability may be higher around Stony Point because of this displacement. Supporting this, a recent study found adult African penguins in Western Cape colonies situated further east (i.e., Stony Point) had a higher body mass compared to those further west (i.e., Robben Island) (Espinaze *et al.* 2020). However, further research with colony-specific estimates of prey availability (e.g., Campbell *et al* . 2019) is required to confirm this, alongside additional monitoring of external factors (e.g., predation rates) that may be driving inter-colony differences

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in survival.

4.2 Reproductive skipping: adaptive or nonadaptive

Our results also indicate that African penguins are not breeding as often as theoretically possible. This finding is common among long-lived seabirds (e.g., Jenouvrier *et al* . 2005) and implies African penguins are either making adaptive decisions to avoid reproductive costs some years, and/or that individual-specific constraints are limiting the ability to breed each year in some individuals. Under adaptive explanations, reproductive skipping should be beneficial, increasing survival and/or future breeding probabilities (Williams 1966). On the contrary, our results show that individuals skipping reproduction had a lower probability of breeding the next year and no survival gain compared to breeding individuals. This suggests reproductive skipping in African penguins is driven by non-adaptive individual-specific constraints e.g. higher quality individuals are more likely to breed and remain breeders (Lescroël *et al.* 2009; Jenouvrier *et al.* 2015).

Supporting this, inter-individual differences in physiology and behaviour of African penguins have previously been noted. For example, some individuals travel further and dive more often (Campbell *et al.* 2019; Traisnel & Pichegru 2019), which may indicate inter-individual differences in foraging efficiency. This is a key driver of inter-individual variation in breeding propensity in Adélie penguins (*Pygoscelis adeliae*) (Lescroël *et al.* 2010), and may drive similar trends in African penguins, with more efficient foragers better able to meet the energetic requirements of reproduction.

Variation in other individual-level traits that can influence breeding success, like aggression (Traisnel & Pichegru 2018) or age (Kappes*et al* . 2021), may also interact with individual quality to affect reproductive skipping. Global declines of African penguins may be driving reduced availability of breeding partners, leaving some (e.g., more experienced or high quality) individuals better placed to retain mates or nest sites, or to find a new breeding partner after divorce or mate mortality (Bruinzeel 2007). However, further individual-level monitoring would be required to determine the drivers of variation in reproductive skipping in African penguins.

4.3 Inter-colony variation in breeding probability

The recent population trend for African penguins at Stony Point has generally been positive while that at Robben Island has been negative, but the drivers of this difference have not been fully explored (Sherley*et al* ., 2020). We indentified clear differences in survival and breeding propensity between the two colonies, drivers that likely underpin these divergent population trends. Overall, individuals at Stony Point had higher adult survival and a higher probability of breeding than those at Robben Island, with breeders at Stony Point also more likely to remain in a breeding state and nonbreeding individuals (including prebreeders) more likely to transition into a breeding state (Figure 5). Trends over time indicate this difference is growing, with an increasing presence of reproductive skipping behaviour over time at Robben Island (Figure 4a). Notably the one occasion at Robben Island where breeding individuals were more likely to skip reproduction the following year than to remain breeders (Figure 4a) coincided with the lower encounter rates in 2020 (Figure 2), likely due to reduced monitoring during the Covid-19 pandemic; this may have led to an overestimation of reproductive skipping rates in this year.

The presence of variation in breeding propensity over time suggests reproductive skipping here is not purely driven by the individual constraints of lower quality individuals, but implicates external drivers that differ between colonies. In other seabirds, food availability is a prominent driver of reproductive skipping (Gauthier-Clerc *et al.* 2001). Despite this, and previous work linking food availability to lower reproductive output in African penguins (Sherley *et al.* 2013, 2018, Campbell *et al* . 2019), this analysis did not find support for food abundance as a driver of reproductive skipping in African penguins. As previously discussed, this may be explained by colony specific food availability not being fully accounted for in this study, with colonies not responding as expected based on the more general prey abundance estimates (e.g., Sherley *et al* . 2013). Alternatively, food availability may only impact African penguin breeding after they have made the decision to breed (e.g., impacting offspring survival, but not the likelihood of attempting to breed). However, disentangling this relationship requires future study with colony-specific measures of prey availability, along

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with additional years of monitoring to improve the estimates of the transition parameters and better capture the full variation in breeding decisions and how they relate to food availability.

Nevertheless, recent research highlighting inter-colony variation in African penguin metrics – such as the higher adult body mass at Stony Point than nearby Western Cape colonies (Espinaze *et al.* 2020) – may help us understand these differences in breeding propensity. In king penguins, individuals will abandon breeding attempts when body mass drops below a certain threshold (Gauthier-Clerc *et al.* 2001), highlighting this as a potential driver of higher breeding propensity at Stony Point. Penguin chicks at Stony Point have also been found to have lower levels of corticosterone (a stress hormone) than chicks at Robben Island (Scheun *et al.* 2021). If this is also true of the adults, this could be a key proximate-level driver of reproductive skipping, with elevated stress due to factors like low food availability causing disruption of the endocrine control of breeding (Kitaysky *et al.*2007; Bókony *et al.* 2009; Crossin *et al.* 2013). These inter-colony differences in stress have been linked to an irregular anthropogenic presence at Robben Island (e.g., researcher presence, some limited tourism, and anthropogenic noise) compared to Stony Point (e.g., regular, high volumes of tourists confined to boardwalks; Scheun*et al.* 2021). Whether variations in localised food availability also contribute to these differences is as yet unclear; further monitoring of stress hormones in relation to external factors (e.g., prey availability) and reproductive skipping could confirm this to better inform our understanding of inter-colony differences and improve population management.

In conclusion, we reveal key insights into African penguin demography, providing the first evidence of reproductive skipping in this species. Penguins are breeding less than theoretically possible, with reduced breeding propensity driven predominantly by individual-specific constraints. We also present clear inter-colony differences: individuals at Robben Island are responding more negatively to declining food availability and are characterised by lower survival and a lower breeding propensity than those at Stony Point. These differences highlight a need for a more detailed understanding of the localised drivers of these differences in population dynamics and imply a greater need for conservation action at Robben Island, beginning with actions to improve access to prey.

Figure Legends

Figure 1. Study site locations (*) at Robben Island and Stony Point in the Western Cape, South Africa, in relation to Cape Town (⟩).

Figure 2. Time-dependent encounter probabilities for adult African penguins at (left) Stony Point and (right) Robben Island between 2014 and 2020, taken from the best overall model (model C36, Table A3). Error bars represent 95% confidence intervals.

Figure 3. Observed (points) and predicted (black lines) survival probabilities of adult African penguins at Robben Island and Stony Point in relation to annual Sardine spawner biomass, taken from the best overall model (model C36, Table A3). Error bars and dotted lines represent 95% confidence intervals of observed and predicted estimates respectively.

Figure 4. Time-dependent probability of transition out of (top) breeder, (middle) nonbreeder, and (bottom) prebreeder states for adult African penguins at Stony Point and Robben Island between 2013–14 and 2019–20, taken from the best overall model (model C36, Table A3). Error bars represent 95% confidence intervals.

Figure 5. Graphical representation of the probabilities (+- SE) of transitioning between breeding states in African penguins based on multistate models. Estimates are taken from the constant model (model C30, Table A3).

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Data availability statement

The data underlying this article will be made available on Dryad upon acceptance for publication.

Competing interests

The authors declare no competing interests

Author contributions

R.B.S. and J.L.G. conceived the study; J.L.G., B.J.B., P.J.B., K.L., C.M., A.M., N.J.P., L.J.W. and R.B.S. contributed to data collection; R.B.S., K.L. and P.J.B. set up the PIT project; B.J.B., K.L. and L.J.W collated the databases; K.L. manages the PIT project; R.B.S., K.L. and P.J.B. obtained the funding; F.L. analysed the data and made the figures, with help and guidance from J.L.G. and R.B.S.; F.L. wrote the first draft of the manuscript; all authors contributed to revisions and gave final approval for publication.

Appendix

Table A1: Number of African penguins *Spheniscus demersus*marked each year with passive integrated transponders (PIT tags) in each colony, organised by breeding state.

Robben Island	Robben Island	Robben Island	Stony Point	Stony Point
Year	Breeder	Nonbreeder (prebreeder)	Breeder	Nonbreeder (prebreeder)
2013	44	0	42	0
2014	25	0	31	2
2015	70	10	77	18
2016	58	20	114	63
2017	67	29	39	15
2018	0	0	0	0
2019	45	6	30	0
2020	8	5	79	2
Total	317	70	412	100

Table A2. Detailed goodness-of-fit results for the general (JMV) model calculated using the 'RMark' package in R.

Test	Stat	DF	P value
Test3Gsr	16.3	18	0.574
Test3Gsm	54.6	30	0.004
Test3Gwbwa	16.9	9	0.05
TestMltech	6.8	3	0.078
TestMitec	24.3	5	<0.001
Overall	115.6	65	<0.001

Table A3. Full model results from the multistate mark-recapture models created in RMARK to assess encounter, survival, and transition (breeding propensity) probabilities for African penguins marked with passive integrated transponders and encountered at Robben Island and Stony Point between 2013 and 2020.

A: Recapture

Model No.	Recapture	Survival	Transition	k	QAICc	[?]QAICc	QDeviance
A10	Time*C+St	Time*C*St	Time*C*St	100	35744.49	0.00	33631.59
A21	Tsm+St	Time*C*St	Time*C*St	88	35750.86	6.36	33664.33
A12	Time+C+St	Time*C*St	Time*C*St	94	35751.10	6.61	33651.42
A20	Tsm+C+St	Time*C*St	Time*C*St	89	35751.91	7.41	33663.19
A15	Tsm*C+st	Time*C*St	Time*C*St	90	35754.10	9.60	33663.19
A17	Tsm*St	Time*C*St	Time*C*St	90	35754.39	9.90	33663.49
A18	Tsm*St+C	Time*C*St	Time*C*St	91	35755.61	11.12	33662.52
A13	Time+St	Time*C*St	Time*C*St	93	35759.99	15.49	33662.51
A16	Tsm*C*St	Time*C*St	Time*C*St	96	35766.55	22.06	33662.48
A9	Time*St	Time*C*St	Time*C*St	105	35771.51	27.02	33647.52
A6	Time*C	Time*C*St	Time*C*St	98	35778.96	34.46	33670.47
A8	Time*C*St	Time*C*St	Time*C*St	126	35793.79	49.29	33622.60
A14	Tsm*C	Time*C*St	Time*C*St	88	35808.66	64.16	33722.13
A2	Tsm	Time*C*St	Time*C*St	86	35814.60	70.11	33732.44
A19	Tsm+C	Time*C*St	Time*C*St	87	35815.83	71.34	33731.49
A11	Time+C	Time*C*St	Time*C*St	92	35816.05	71.55	33720.76
A5	C+St	Time*C*St	Time*C*St	88	35821.74	77.25	33735.21
A3	C*St	Time*C*St	Time*C*St	90	35825.25	80.76	33734.35

Model No.	Recapture	Survival	Transition	k	QAICc	[?]QAICc	QDeviance
A4	St	Time*C*St	Time*C*St	87	35832.35	87.86	33748.01
A7	Time	Time*C*St	Time*C*St	91	35835.42	90.93	33742.33
A1	C	Time*C*St	Time*C*St	86	35957.83	213.33	33875.67

Notes: K = the number of estimated parameters, QAICc = Akaike Information Criterion corrected for over-dispersion and small sample size, and [?]QAICc = the difference in QAICc between the model in question and the best supported model. Interactions between parameters are denoted by (*) and additive effects by (+). In each model, t refers to time dependence, C to the group effect for colony, St to state (prebreeder, nonbreeder, breeder), and tsm to the grouping of recapture years by ground reader placement. Combined annual Anchovy and Sardine spawner biomass was referred to as 'Fish', and separated data by 'Anchovy' and 'Sardine' respectively. Recapture models were created with survival and transition in their most general form (time, colony and state dependent). Survival was then modelled using the best recapture model and holding transition in its most general form. Transition models were then modelled using the best recapture and survival model.

Table A3. Cont.

B: Survival

Model No.	Recapture	Survival	Transition	k	QAICc	[?]QAICc	QDeviance
B22	Time*C+St	Sardine*C	Time*C*St	62	35696.46	0.00	33665.99
B32	Time*C+St	Time*C	Time*C*St	72	35697.81	1.35	33645.95
B24	Time*C+St	Sardine*C+St	Time*C*St	64	35699.00	2.55	33664.27
B23	Time*C+St	Sardine*C*St	Time*C*St	70	35700.61	4.15	33653.05
B34	Time*C+St	Time	Time*C*St	65	35701.89	5.43	33665.02
B38	Time*C+St	Time+C	Time*C*St	66	35703.38	6.93	33664.38
B33	Time*C+St	Time*C+St	Time*C*St	74	35704.18	7.72	33648.02
B13	Time*C+St	Fish*C	Time*C*St	62	35704.86	8.40	33674.39
B10	Time*C+St	C	Time*C*St	60	35704.95	8.50	33678.74
B25	Time*C+St	Sardine	Time*C*St	60	35705.42	8.96	33679.20
B40	Time*C+St	Time+St	Time*C*St	67	35705.86	9.41	33664.73
B7	Time*C+St	Anchovy+C	Time*C*St	61	35705.91	9.45	33677.56
B1	Time*C+St	Anchovy*C	Time*C*St	62	35706.10	9.64	33675.63
B28	Time*C+St	Sardine+C	Time*C*St	61	35706.18	9.73	33677.84
B19	Time*C+St	Fish+C	Time*C*St	61	35706.43	9.98	33678.09
B12	Time*C+St	C+St	Time*C*St	62	35707.04	10.58	33676.57
B39	Time*C+St	Time+C+St	Time*C*St	68	35707.24	10.78	33663.96
B8	Time*C+St	Anchovy+C+St	Time*C*St	63	35707.41	10.95	33674.81
B15	Time*C+St	Fish*C+St	Time*C*St	64	35707.51	11.05	33672.78
B4	Time*C+St	Anchovy	Time*C*St	60	35708.03	11.57	33681.81
B30	Time*C+St	Sardine+St	Time*C*St	62	35708.09	11.63	33677.62
B20	Time*C+St	Fish+C+St	Time*C*St	63	35708.13	11.67	33675.53
B16	Time*C+St	Fish	Time*C*St	60	35708.19	11.73	33681.97
B18	Time*C+St	Fish*St+C	Time*C*St	65	35708.24	11.78	33671.37
B26	Time*C+St	Sardine*St	Time*C*St	64	35708.35	11.89	33673.62
B3	Time*C+St	Anchovy*C+St	Time*C*St	64	35708.48	12.02	33673.75
B29	Time*C+St	Sardine+C+St	Time*C*St	63	35708.49	12.03	33675.89
B31	Time*C+St	St	Time*C*St	61	35708.51	12.05	33680.16

Model No.	Recapture	Survival	Transition	k	QAICc	[?]QAICc	QDeviance
B6	Time*C+St	Anchovy*St+C	Time*C*St	65	35708.60	12.14	33671.73
B27	Time*C+St	Sardine*St+C	Time*C*St	65	35708.61	12.15	33671.75
B11	Time*C+St	Colony*St	Time*C*St	64	35708.88	12.43	33674.15
B17	Time*C+St	Fish*St	Time*C*St	64	35709.52	13.07	33674.79
B5	Time*C+St	Anchovy*St	Time*C*St	64	35710.11	13.65	33675.38
B9	Time*C+St	Anchovy+St	Time*C*St	62	35710.24	13.78	33679.77
B21	Time*C+St	Fish+St	Time*C*St	62	35710.56	14.10	33680.09
B14	Time*C+St	Fish*C*St	Time*C*St	70	35710.81	14.35	33663.25
B2	Time*C+St	Anchovy*C*St	Time*C*St	70	35712.63	16.17	33665.07
B36	Time*C+St	Time*St	Time*C*St	79	35722.45	26.00	33655.50
B37	Time*C+St	Time*St+C	Time*C*St	80	35724.11	27.65	33654.98
B35	Time*C+St	Time*C*St	Time*C*St	100	35744.49	48.04	33631.59

Table A3. Cont.

C: Transition

Model No.	Recapture	Survival	Transition	k	QAICc	[?]QAICc	QDeviance
C36	Time*C+St	Sardine*C	Time*C*St	62	35696.45	0.00	33665.98
C34	Time*C+St	Sardine*C	Time*C+St	36	35727.94	31.48	33752.08
C30	Time*C+St	Sardine*C	C*St	26	35731.43	34.97	33776.20
C3	Time*C+St	Sardine*C	Anchovy*C*St	32	35734.51	38.06	33766.93
C6	Time*C+St	Sardine*C	Anchovy*St+C	27	35736.92	40.47	33779.64
C13	Time*C+St	Sardine*C	Fish*C*St	32	35737.15	40.69	33769.56
C31	Time*C+St	Sardine*C	C+St	24	35737.32	40.86	33786.19
C22	Time*C+St	Sardine*C	Sardine*C*St	32	35737.90	41.45	33770.32
C39	Time*C+St	Sardine*C	Time+C+St	30	35738.31	41.85	33774.85
C27	Time*C+St	Sardine*C	Sardine+C+St	25	35738.76	42.30	33785.58
C18	Time*C+St	Sardine*C	Fish+C+St	25	35739.33	42.87	33786.15
C16	Time*C+St	Sardine*C	Fish*St+C	27	35739.35	42.89	33782.06
C8	Time*C+St	Sardine*C	Anchovy+C+St	25	35739.37	42.91	33786.19
C14	Time*C+St	Sardine*C	Fish*C+St	26	35740.20	43.74	33784.97
C4	Time*C+St	Sardine*C	Anchovy*C+St	26	35740.26	43.80	33785.02
C23	Time*C+St	Sardine*C	Sardine*C+St	26	35740.39	43.93	33785.16
C37	Time*C+St	Sardine*C	Time*St+C	42	35741.40	44.95	33753.07
C25	Time*C+St	Sardine*C	Sardine*St+C	27	35741.65	45.19	33784.36
C29	Time*C+St	Sardine*C	St	23	35744.48	48.03	33795.40
C40	Time*C+St	Sardine*C	Time+St	29	35745.31	48.86	33783.91
C5	Time*C+St	Sardine*C	Anchovy*St	26	35745.41	48.95	33790.18
C28	Time*C+St	Sardine*C	Sardine+St	24	35746.47	50.01	33795.34
C9	Time*C+St	Sardine*C	Anchovy+St	24	35746.47	50.01	33795.34
C19	Time*C+St	Sardine*C	Fish+St	24	35746.50	50.05	33795.37
C15	Time*C+St	Sardine*C	Fish*St	26	35747.28	50.83	33792.05
C24	Time*C+St	Sardine*C	Sardine*St	26	35749.57	53.11	33794.34
C35	Time*C+St	Sardine*C	Time*St	41	35751.10	54.64	33764.84
C33	Time*C+St	Sardine*C	Time*C	34	35798.06	101.60	33826.34
C2	Time*C+St	Sardine*C	Anchovy*C	24	35844.31	147.85	33893.18
C38	Time*C+St	Sardine*C	Time+C	28	35844.57	148.12	33885.23

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Model No.	Recapture	Survival	Transition	k	QAICc	[?]QAICc	QDeviance
C12	Time*C+St	Sardine*C	Fish*C	24	35846.48	150.02	33895.35
C32	Time*C+St	Sardine*C	Time	27	35853.20	156.74	33895.91
C10	Time*C+St	Sardine*C	C	22	35855.38	158.92	33908.34
C26	Time*C+St	Sardine*C	Sardine+C	23	35856.14	159.68	33907.06
C7	Time*C+St	Sardine*C	Anchovy+C	23	35856.82	160.37	33907.74
C17	Time*C+St	Sardine*C	Fish+C	23	35857.27	160.82	33908.19
C21	Time*C+St	Sardine*C	Sardine*C	24	35857.50	161.05	33906.37
C1	Time*C+St	Sardine*C	Anchovy	22	35867.86	171.40	33920.82
C11	Time*C+St	Sardine*C	Fish	22	35868.76	172.30	33921.72
C20	Time*C+St	Sardine*C	Sardine	22	35870.23	173.78	33923.20