

Supporting Information. Sex-biased survival contributes to population decline in a long-lived seabird, the Magellanic penguin. N. J. Gownaris and P. D. Boersma. *Ecological Applications*. 2018.

Appendix S1: Additional Methodological Details

Text S1: Additional Details, Literature Search

We conducted a Web of Science literature search using the terms “mark-recapture” or “mark recapture” and “seabird”, restricted to the range of 2005-2015 (conducted in September of 2016). We chose this time frame to represent the decade following publication of Nichols et al. (2004) and Pradel (2005), which both offered options for situations in which sex is not known for all individuals (additional options published since this time; e.g. Laake 2013). This search resulted in 81 publications. We reviewed the abstract of each publication to ensure relevance based on the following criteria: 1) focused on seabirds; theoretical studies were not included, 2) mentioned the use of a mark-recapture model, 3) estimated demographic parameters (survival, emigration, or breeding propensity) of juveniles and/or adults. Fifty-nine publications met these criteria, but only 12 mentioned the consideration of sex (references in boldface in the list below). Of these 12 studies, nine (references with an asterisk in the list below) found sex-driven demographic heterogeneity.

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Text S2: Additional Details, Mark-Recapture Model Development

Hidden Markov Models assume that state transitions can be described by a first-order Markov process where an individual's current state is dependent on its previous state (Laake 2013). The *marked* likelihood is calculated using forward probability vectors and the Automatic Differentiation Model Builder (Laake 2013, Laake et al. 2013) and 95% confidence intervals are estimated using the Hessian matrix (Johnson et al. 2016). In addition to the traditional model parameters survival (Φ ; Phi), recapture (p), and transition (Ψ ; Psi), *marked* includes a parameter for the initial state distribution (π or π_i ; in this case, sex and breeding state) and a parameter for the probability that an individual's state can be assessed with certainty (δ or delta).

We sexed 57% of individuals with certainty using one of the following methods: 1) genetic testing, 2) cloaca size around egg laying (Boersma and Davis 1987), 3) breeding behavior (copulation, etc.), or 4) bill size (male bill depth ≥ 2.24 ; females < 2.24). We most commonly sexed individuals using bill size, which previous work has shown to be a reliable sexing method. Discriminant function analyses found that Magellanic penguins were sexed correctly using only bill depth at six colonies in 95% of cases (Bertellotti et al. 2002) and at Punta Tombo in 97% of cases (Boersma, unpublished data). Excluding the 43% of unsexed individuals in our study from the analysis could bias sex-specific survival results (Nichols et al. 2004). To account for the individuals that were not sexed, we treated sex as an uncertain state with a zero probability of transition.

We train all field season volunteers to visually sex Magellanic penguins. Visual sexing is based on visual cues compiled on each individual, including their bill depth (males have noticeably deeper bills), frons shape (males have steeper-sloped frons), body size (males are larger), and aggressiveness (males tend to be more aggressive). We correctly sex Magellanic penguins visually in most cases ($>86\%$ accuracy in any given year; $>98\%$ across all years; Boersma, unpublished data), and rely on these data to track survey-estimated trends in colony sex ratio, but excluded this method of sexing from our model to avoid misclassification. We calculated accuracy as the percentage of visual assessments that matched the sex we assigned to an individual with certainty (methods 1-4 above), as 60% of individuals were sexed both visually and with certainty over their lifetime. The sex ratio of resighted birds was similar whether we included (676 females and 1,798 males; sex ratio = 0.73) or excluded (471 female and 1,422 male; sex ratio = 0.75) individuals sexed only visually.

We categorized individuals into four breeding states: pre-breeder (P), breeder (B), non-breeder (N), or uncertain (u; breeding state unknown). The model included two unobservable states: unobservable pre-breeder (X) and unobservable non-breeder (Y). All individuals were in

the pre-breeding state at initial release (Appendix S3: Figure S1). Pre-breeders could not be assigned with certainty after individuals returned from their first year at sea (age ≥ 1), due to loss of juvenile plumage. Male Magellanic penguins sometimes move into nests with females that are incubating eggs from another male. Therefore, the criteria we used for certain breeders were more stringent for males than for females. We considered females to be breeders if they were seen with either an egg or a chick in a breeding season. We considered males and unsexed individuals to be breeders if we sighted them with a chick or incubating eggs in a breeding season. If we sighted them without eggs or chicks, or with eggs that they were not incubating, we considered them to be in an unknown breeding state (u).

Of more difficulty was assigning individuals to the non-breeder state with certainty. Though we regularly conducted searches for banded breeders, we may have missed some nests (e.g. in less dense, peripheral areas of the colony or in deep burrow nests). As a result, we cannot know the breeding state of individuals sighted while wandering through the colony. We conducted preliminary analyses to estimate this uncertainty and to develop criteria that allowed us to assign some individuals to the non-breeding state with certainty. These analyses showed that we had a 32% chance of sighting a known breeder without eggs or chicks at least once that season. Because we only sighted 12% of banded individuals more than once in a season, there was a high chance of incorrectly assigning individuals to the non-breeding state, supporting the need for breeding state uncertainty in the model. When we could not categorize individuals as either breeders or non-breeders, we gave them an unknown breeding state. We considered males and females to be non-breeders if they met all criteria in at least one of the two following categories:

Criteria Set 1: 1) of breeding age (≥ 4), 2) sighted at least two times without an egg or chick in October – December, 3) never sighted with an egg or chick during that breeding season.

Criteria Set 2: 1) of breeding age (≥ 4), 2) sighted in only one nest that breeding season, 3) never sighted with eggs and the field crew stopped following nest because there were no eggs or chicks by mid-November.

We imposed the following breeding transition constraints based on the biology of the species and inherent state characteristics: 1) no transitions to the breeding state until age four (1% of males and 9% of females start breeding at age four; Boersma et al. 2013), 2) no transitions from pre-breeding states to non-breeding states, 3) no transitions from breeding or non-breeding states to pre-breeding states, 4) transitions between observable pre-breeder and unobservable pre-breeder were equal ($\Psi_{XP} = \Psi_{PX}$) (Appendix S3: Figure S1).

Complex multi-state models often result in many unidentifiable parameters, particularly when parameters are time-variant and when uncertain or unobservable states are included (Kendall and Nichols 2002, Hunter and Caswell 2009, Pradel 2009, Bailey et al. 2010). Preliminary tests suggested that, in our system, parameter estimability was highly sensitive to the specification of the certainty parameter (δ) and the breeding state transition parameter (Ψ). Inclusion of age, time, or sex in the specification of Ψ resulted in many parameters with

confidence intervals spanning [0,1]. Therefore, Psi was specified to depend only on the state an individual was in and the state an individual was transitioning to (Appendix S3: Figures S1-S2).

Specification of delta was based on the field season protocol and the criteria used to develop the recapture histories (Appendix 2). All individuals were assumed to be pre-breeders when banded as chicks, but to not be identifiable as pre-breeders with certainty after initial capture ($\delta = 1$ at age 0 and $\delta=0$ at ages ≥ 1 for this state), as individuals greater than a year molt into adult plumage. Males and females varied in how often their sex was assessed due to differences in timing of colony attendance and breeding behavior. Because breeding state definitions varied with sex and breeding state, so did the breeding state certainty parameter (Appendix 2; Figure S2).

Text S3: Additional Details, Mark-Recapture Model Selection

We tested for goodness-of-fit using the median c-hat (\hat{c}) approach in the Program MARK (Cooch and White 2013) and a modified version of the model created in *marked*, as MARK does not allow for two levels of uncertainty in state assignment. This model assumed certainty in breeding state and grouped all unobservable individuals into one state. C-hat values from 1-10 were simulated using 10 intermediate points, each with 10 replicates. The modified general model had a c-hat of 2.22, within the range of acceptable values (c-hat < 3.00 ; Lebreton et al. 1992, Cooch and White 2013). We used quasi-AIC (QAIC) to compare candidate models. Quasi-AIC is the likelihood of a model divided by its variance inflation factor and results in similar biological conclusions to those reached when all causes of overdispersion can be modelled explicitly (Richards 2008).

We conducted model selection in three phases; formulae for delta and Psi were held constant (Figure S2). During Phase 1, we compared all possible combinations of Phi (all additive combinations of age, sex, and time) and p formulae (all additive combinations of breeding state, sex, and time). Data were too sparse to include interaction terms without high rates of inestimable parameters. The most general candidate model we tested had the greatest support (Appendix S2: Table S1). The next best model considered only additive time and age effects in survival (i.e. no sex effects), but this model was on the order of 10^{11} times less likely than the best supported model according to its Akaike weight. Removing variation with time or age had even larger effects on QAIC than did removing sex.

During Phase 2, we modified the best-supported model from Phase 1 to address parameter estimation issues, particularly due to data sparseness for older-aged individuals, by creating an age class-based model. This modification was based on preliminary analyses suggesting clear age class structure in survival estimates and resulted in three stages: juveniles (fledging to age 1), adult (ages 1-18), and elder individuals (ages ≥ 19). Sex was included as an additive variable in the model and we tested how removing sex affected model fit. Based on preliminary analyses, juvenile survival varied with year in all models. We tested a subset of

additive year and age combinations (including survival as a linear function of age) for the adult and elder age classes (Appendix S2: Table S2; Appendix S3: Figure S2).

In all cases, the modified age class models developed in Phase 2 had QAICs that were lower than that of the general model. In the best supported model survival varied with sex, with year for juveniles (fledging to age 1), with year and age for adults survival (1-18 years), and as a linear (decreasing) function of age for elder individuals (≥ 19 years) (Table S2). The support for this model was 10^{32} times greater than the most general model ($\Delta_{QAIC}=149$). Removing sex from the survival specification resulted in Δ_{QAIC} of greater than 50 for all age class models (Table S2).

During Phase 3, we added breeding state considerations to the specification of Phi (Appendix S2: Table S2; Appendix S3: Figure S2). We tested three breeding state groupings: 1) BS1 grouped all individuals not breeding (observable and unobservable pre-breeders and non-breeders) separately from all individuals breeding (breeders), 2) BS2 grouped all individuals that had not yet successfully bred (observable and unobservable pre-breeders) separately from those that had begun breeding (breeders and observable and unobservable non-breeders), 3) BS3 was comprised of three separate groups: individuals that had not yet bred (observable and unobservable pre-breeders), individuals that were breeders (breeders), and individuals that had begun breeding but were not breeding in a given year (observable and unobservable non-breeders). The models developed in Phase 3 all had a lower QAIC than models that did not consider breeding states. The three breeding state groupings (BS1, BS2, and BS3) showed similar support, but the best-supported model was that using BS2 in the Phi specification (Appendix S2: Table S2).

Text S4: Additional Details, Population Matrix Model

We used an initial population size of 300,000 individuals of each sex, as this would have been the approximate size of the colony in 1990 based on an initial population size of 314,000 breeding pairs in 1987 and an annual decline of 1.8% (Rebstock et al. 2016). We assumed an ASR of 0.5 at the start of the simulation. The survival of individuals aged 30 was set to zero, so this age acted as an absorbing state. Individuals older than 30 are rarely sighted at the colony and the oldest known-aged penguin in the study was a 32-year-old male (Boersma, unpublished data). We defined the hatching sex ratio based on the proportion of male offspring and assumed that it was equal to 0.50 and remained at 0.50 until fledging. A small sample size of genetically sexed chicks validated this assumption (Koehn et al. 2016). Reproductive success was based on nest check data collected at the colony over the same period covered by the mark-recapture analysis and was year-specific for the time-variant matrix (average 0.50 ± 0.26 chicks/pair; Rebstock and Boersma 2017).

Using the time-invariant matrix \mathbf{M}_ϕ , the population growth rate (λ) stabilized at 0.895 after 39 years, remaining at this rate through the final simulation of 100 years (i.e. the asymptotic value) with a stable stage adult sex ratio of 0.723. This model suggests an

equilibrium population that is declining by 10.5% annually, which is a faster rate of decline than we measured in the field. This discrepancy could result from a combination of two factors 1) we underestimate effective population decline when we depend on survey data, as an increasing proportion of active nests are likely to represent unmated males and 2) there is immigration to the colony not accounted for by our model.

Appendix S1 References

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