Integrated population model of Antipodean albatross for simulating management scenarios

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Cover Notes

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EXECUTIVE SUMMARY

Antipodean albatross *Diomedea antipodensis antipodensis* is endemic to New Zealand, with the quasi-totality of the population nesting on Antipodes Island. The species is classified as Nationally Critical due to a potential demographic decline. Threats to the population include incidental mortality in fisheries, climate change, and depredation by exotic species.

The objective of this project was to provide a tool that allows stakeholders to explore the potential impact of threats and the demographic outcomes of management strategies. Using the tool, simulations of the demographic impact of different scenarios may be carried out so that management strategies can be assessed and prioritised.

A small subset of the population of Antipodean albatross has been studied since 1994, and these field data were used to perform the simulations. A Bayesian integrated population model was developed to estimate the main demographic parameters of the population. The model considered detectability of individuals, inter-annual variability, movements in and out of the study area, and data censoring; it was fitted using the software Stan.

The model results indicated that the probability of detecting individuals decreased from 2007 onwards, but this finding did not explain the observed decline in adult annual survival. The estimated annual survival rate for females was estimated to decline from 0.947 (95% c.i.: 0.914 – 0.974) in the period from 1994 to 2004, to 0.882 (95% c.i.: 0.814 – 0.94) after 2005. Estimated survival for males was higher, at 0.946 (95% c.i.: 0.913 – 0.972) and 0.927 (95% c.i.: 0.887 – 0.961) for the two periods. Breeding success also declined between the two periods, from 72.4% (95% c.i.: 65.8% – 78.6%) from 1994 to 2004 to 63.7% (95% c.i.: 53.4% – 73%) subsequently.

Under the current scenario, simulations suggest a significant decline of the population, with an annual growth rate of -4.84% (95% c.i.: -6.07% – -3.65%). Limitations in the data and in the model assumptions may cause the decline to be overestimated; however, the results raise concerns about the sustainability of the population.

The simulation tool is aimed to assist conservation managers with the prioritisation of management strategies to mitigate threats to the Antipodean albatross population and to guarantee the persistence of this species.

1. INTRODUCTION

The seabird species Antipodean albatross (*Diomedea antipodensis antipodensis*) is endemic to New Zealand and consists of two subspecies, Antipodean albatross (*D. a. antipodensis*) and Gibson's albatross (*D. a. gibsoni*). The subspecies Antipodean albatross breeds almost exclusively on Antipodes Island, with a few pairs breeding on Chatham and Campbell islands, whereas Gibson's albatross breeds on Auckland Island. The species is classified as Endangered by the International Union for Conservation of Nature (BirdLife International 2018), and each subspecies is classified individually as Nationally Critical in New Zealand (Robertson et al. 2017).

The population of Antipodean albatross is exposed to a number of threats, at sea and on land. They are caught incidentally in surface-longline fisheries in New Zealand waters and globally (Richard & Abraham 2017). Chicks used to be depredated by mice at the nest, although mice have been eradicated from Antipodes Island since 2016. Climate change may also impact the population indirectly, increasing heat stress to chicks and affecting the distribution or abundance of prey species.

On Antipodes Island, a 29-ha (0.29-square kilometre) area of the Antipodean albatross population has been monitored every year since 1994, except in 2006. Field data from this area (Elliott & Walker 2020) and quantitative modelling (Edwards et al. 2017) suggest a population decline since 2007, via a decline in female survival and in breeding success, and an increase in recruitment age. Tracking data of individual at-sea movements also suggest a potential change in the foraging grounds over time (Elliott & Walker 2020).

Tracking at-sea movements also allowed the identification of fisheries with the highest overlap with the species (Bose & Debski 2020). A number of mitigation techniques exist to reduce the level of incidental captures in fisheries and are already in place in a number of fisheries, in New Zealand and worldwide (Løkkeborg 2011).

The main objective of this project was to develop an online tool to facilitate the prioritisation of management strategies around population threats. The online tool allows the running of simulations of the fate of the population under different scenarios, leading to the identification of strategies with the highest positive impact on the population. The simulations rely on estimates of the main demographic parameters of this subspecies. A Bayesian integrated population model was developed for this purpose, based on the individual capture-recapture data that have been collected in the study area on Antipodes Island since 1994.

2. METHODS

The Antipodean albatross subspecies breeds almost exclusively on Antipodes Island (Agreement on the Conservation of Albatrosses and Petrels 2009). When breeding, a single egg is laid on a nest consisting of a low pedestal build of soil and vegetation, often re-used between breeding attempts. It takes a year for an egg to produce a fledgling. For this reason, adults can only breed every second year when successful. Fledglings spend the first few years at sea before returning to the colony, and subsequently spend another year or more before breeding for the first time.

Since 1994, a 29-ha (0.29-square kilometre) area on Antipodes Island has been surveyed every year, except in 2006; the most recent survey was in 2021. Survey visits to the island were generally conducted in January, so that the outcome of the previous year's breeding attempts could be observed, and new breeding attempts could also be recorded. Each visit was on average for a month to allow sufficient time to survey the birds present and to band any new birds in the study area. Due to the remoteness of the island and its limited accessibility, logistic constraints led to variation in the exact timing and length of visits between years.

The data collected in the field consist of the date and location of detected banded individuals at the site, their breeding status and stage, and their sex when identifiable.

Additionally, a buffer around the study area was frequently visited, in addition to two other blocks on the island. In these areas, the sightings and breeding status of banded individuals were also recorded, and identified as being outside the study area. A description of the field data is presented in Edwards et al. 2017

The data were aggregated to create individually- and annually-based capture histories, representing the state of individuals each year between 1994 and 2021. Individuals were categorised into three age classes: juvenile (between fledging and first return to the colony), pre-breeder (from first return to first breeding at the colony), and adult (after first breeding). Eight observed states were represented:

1. adult breeding inside the study area;
2. adult non-breeding inside the study area;
3. adult outside the study area (breeding or not);
4. pre-breeder inside the study area;
5. pre-breeder outside the study area;
6. juvenile;
7. dead;
8. not seen.

Adults sighted both inside and outside the study area one year were considered inside the study area. Adults only sighted outside the study area were not split between breeders and non-breeders as their breeding status cannot be identified precisely (especially for birds seen early in the season). Because surveys of the study area overlapped between the end of the previous breeding season and the beginning of the next one, the aggregated data were prepared to represent the status of the population just before breeding occurs; i.e., chicks of the current breeding year first appear in the prepared data the following year after fledging (if successful). Only birds banded within the study area were included in the final dataset.

Nest success was recorded at the nest level, as the nesting individuals might not necessarily be seen, and nests were considered successful if they produced a fledgling. A successful nests could either have a chick being very close to fledging at the last observation, or empty but showing indications of recent breeding activity without showing any sign of failure (e.g.; broken shells, dead body parts).

2.1 Integrated population model

To estimate the main demographic parameters of the population of Antipodean albatross, a multi-state Bayesian capture-recapture model was developed. This type of model aims to alleviate the main biases in the data, which are common to most population survey data.

The state of an individual can be unknown, and an individual may be undetected but still alive. Individuals may be undetected in a given year for several reasons. They could be at sea, such as juveniles, adults previously breeding successfully or on a "sabbatical" year, or breeding adults on a foraging trip may not be detected during short visits to the island. Undetected individuals could also be present at the colony, but outside the study area.

For these reasons, the "actual" state of individuals was considered as a latent variable in the model, with year-to-year transitions between the states determined by explicit biological rules. For example, an adult cannot become a juvenile, or an adult breeding successfully cannot breed again the following year. In addition, an observation process was considered, linking the latent state to the observed state, and determined by both the survey effort and the birds' behaviour.

2.1.1 Latent states

A total of eight latent states were considered in the model, different from the observed states:

1. adult breeding inside the study area;
2. adult breeding outside the study area;
3. adult non-breeding inside the study area;
4. adult non-breeding outside the study area;
5. pre-breeder inside the study area;

6. pre-breeder outside the study area;
7. juvenile;
8. dead.

The transition matrix between the eight latent states required specifying the probability of being in each latent state given the previous one, representing 64 transition probabilities.

For juveniles (J), pre-breeders (PB), breeding adults (B), and non-breeding adults (NB), the probabilities of changing to a different live state given the previous state were:

$$P(\mathrm{PB}_t|\mathrm{J}_{t-1}) = R_a\phi_{\mathrm{J}}, \tag{1}$$

$$P(\mathrm{B}_t|\mathrm{PB}_{t-1}) = B_a\phi_{\mathrm{PB}}, \tag{2}$$

$$P(\mathrm{B}_t|\mathrm{NB}_{t-1}) = P(\text{breed}|\text{non-breeder})\phi_{\mathrm{s}}, \tag{3}$$

$$P(\mathrm{NB}_t|\mathrm{B}_{t-1}) = \begin{cases} 1 & \text{after a successful breeding attempt,} \\ \big(1 - P(\text{breed}|\text{fail})\big)\phi_{\mathrm{s}} & \text{after a failed breeding attempt,} \end{cases} \tag{4}$$

where t is the year, $\phi_{\{\mathrm{J},\mathrm{PB},s\}}$ the annual survival rate of juveniles, pre-breeders, and adults of sex s, respectively, R_a the probability of a juvenile of age a returning to the colony, B_a the probability of a pre-breeder of age a breeding for the first time, $P(\text{breed}|\text{fail})$ the probability of an adult breeding in a particular year, given it was an unsuccessful breeder the previous year, $P(\text{breed}|\text{non-breeder})$ the probability of an adult breeding in a particular year, given it was a non-breeding adult the previous year.

When the sex was unknown, conditional probabilities were used; e.g., the annual survival rate of an individual of unknown sex was $P(♀)\phi_{♀} + (1 - P(♀))\phi_{♂}$, where $P(♀)$ is the probability that an individual in the study area is a female.

The probabilities of remaining in the same live state from one year to the next were:

$$P(\mathrm{J}_t|\mathrm{J}_{t-1}) = (1 - R_a)\phi_{\mathrm{J}}, \quad (5)$$

$$P(\mathrm{PB}_t|\mathrm{PB}_{t-1}) = (1 - B_a)\phi_{\mathrm{PB}}, \quad (6)$$

$$P(\mathrm{NB}_t|\mathrm{NB}_{t-1}) = \big(1 - P\,(\text{breed}|\text{non-breeder})\big)\phi_{\mathrm{s}}, \quad (7)$$

$$P(\mathrm{B}_t|\mathrm{B}_{t-1}) = \begin{cases} 0 & \text{after a successful breeding attempt,} \\ P(\text{breed}|\text{fail})\phi_{\mathrm{s}} & \text{after a failed breeding attempt,} \\ (1 - P(\text{success}))P(\text{breed}|\text{fail})\phi_{\mathrm{s}} & \text{after an unknown outcome.} \end{cases} \quad (8)$$

In addition, the transition probabilities were multiplied by the probability of moving inside or outside the study area, depending on the state:

$$P(\mathrm{Out}_t|\mathrm{In}_{t-1}) = E_s, \quad (9)$$

$$P(\mathrm{In}_t|\mathrm{Out}_{t-1}) = I_s, \quad (10)$$

$$P(\mathrm{Out}_t|\mathrm{Out}_{t-1}) = 1 - I_s, \quad (11)$$

$$P(\mathrm{In}_t|\mathrm{In}_{t-1}) = 1 - E_s, \quad (12)$$

where E_s is the probability of an individual of sex s moving out of the study area (emigrate), and I_s the probability of an individual of sex s moving into the study area (immigrate).

The probabilities of being dead (D) in a particular year were:

$$P(\mathrm{D}_t|\mathrm{J}_{t-1}) = 1 - \phi_{\mathrm{J}}, \quad (13)$$

$$P(\mathrm{D}_t|\mathrm{PB}_{t-1}) = 1 - \phi_{\mathrm{PB}}, \quad (14)$$

$$P(\mathrm{D}_t|\mathrm{B}_{t-1}) = 1 - \phi_{\mathrm{s}}, \quad (15)$$

$$P(\mathrm{D}_t|\mathrm{NB}_{t-1}) = 1 - \phi_{\mathrm{s}}, \quad (16)$$

$$P(\mathrm{D}_t|\mathrm{D}_{t-1}) = 1. \quad (17)$$

The probability of impossible transitions—e.g., from adult to juvenile or to pre-breeder, from pre-breeder to juvenile, and from dead to alive—were fixed to zero.

The adult annual survival rate was estimated independently for females and males, and was allowed to vary randomly between years, with the survival rate $\phi_{s,t}$ for sex s at year t being defined on the logit scale as:

$$\text{logit}(\phi_{s,t}) = \text{logit}(\bar{\phi_s}) + \epsilon_{s,t} s_s, \tag{18}$$

where $\bar{\phi_s}$ is the mean survival rate across years for sex s, $\epsilon_{s,t}$ is the normally-distributed random effect for each sex and year, and s_s is the sex-specific variability of the random effect among years.

The annual survival rate of juveniles and pre-breeders was assumed to be constant over time, and the same between males and females in the model.

As for adult survival, breeding success, i.e., the probability that a nest produces a fledgling, was also modelled as a random effect over time.

The probability R_a of a juvenile of age a returning to the colony and becoming a pre-breeder was set to 0 at ages below the minimum observed age at first return (3 years), and set to 1 for birds of age 9 and above, as all birds are expected to have returned to the colony by age 9 (G. Elliott, pers. comm.). The age-specific probability of return for birds aged 3 to 8 was modelled as a random effect.

Similarly, the probability B_a of a pre-breeder of age a to become a breeder for the first time was set to 0 for birds under 7 years old, the minimum recorded breeding age. The age-specific probability of first breeding for birds aged 7 to 20 was modelled as a random effect. The probability for birds aged 21 and above was set to be constant to represent the long tail in the distribution of age at first breeding (i.e., some birds take a long time to breed or do not breed)

Both R_a and B_a were dependent on age, but assumed not to vary with year.

2.1.2 Observation process

In the model, latent states are related to observed states via an observation matrix, representing the probability of recording any of the eight observed states given a latent state (one of 8 latent states, different from the observed states).

The probability of detection was estimated separately in the model for:

- breeding adults inside the study area,
- non-breeding adults inside the study area that previously bred successfully,
- other non-breeding adults inside the study area,
- pre-breeders inside the study area,
- adults and pre-breeders outside the study area,
- juveniles (outside the study area by definition),
- dead individuals.

There were only a few recorded observations of juveniles and dead individuals, with all juveniles and most deaths being recorded at sea. For this reason, their detection probability was assumed to be constant among years.

Because year-to-year variations are most likely to reflect the timing and amount of observations on the island, the other detection probabilities were allowed to vary among years, but with the same annual variability among them; they were defined as:

$$\text{logit}(\gamma_{x,t}) = \text{logit}(\gamma_x) + \epsilon_t s, \tag{19}$$

where $\gamma_{x,t}$ is the detection probability of birds of category x at year t, $\text{logit}(\gamma_x)$ the average detection probability for category x among years, ϵ_t the random annual effect of year t for all categories, and s the variability among years for all categories.

For 2006, when the population was not surveyed, all detection probabilities were fixed to zero.

2.1.3 Model fitting

The model was written in the Stan language and fitted in the R statistical package (R Core Team 2019) using the *rstan* library (Stan Development Team 2020).

Stan was chosen over alternatives such as Bugs or JAGS as it implements the no-U-turn sampler (NUTS; Hoffman & Gelman 2014) which improves model convergence and allows fitting times to be reduced by an order of magnitude (from days to hours).

One disadvantage of Stan is that it does not support the direct sampling of discrete parameters. Nevertheless, multi-state models can still be fitted by marginalising discrete latent states, i.e., summing at each time step the likelihood of the observed state over all possible latent states, iteratively over each individual capture history (Yackulic et al. 2020).

The model was fitted using Markov chain Monte Carlo (MCMC) methods, using four chains, for 6,000 iterations, after a burn-in period of 5,000 iterations.

The code of the Stan model is provided in Appendix A.

2.2 Population simulations

The main aim of this project was to provide stakeholders with a tool to simulate the fate of the Antipodean albatross population under different scenarios. For this purpose, an interactive online application written in R and using the Shiny framework was developed.

Because the demographic model does not provide the latent state of individuals at each time step directly due to the marginalisation of discrete latent variables, the initial population structure for the simulations was derived separately. For this purpose, the latent state at each time step for each individual was drawn randomly from the previous state and the observed state. Using Bayes' theorem, the probability of an individual to be in the latent state Π_i given the observed state O is:

$$P(\Pi_i|O) = \frac{P(O|\Pi_i)P(\Pi_i)}{P(O)}, \tag{20}$$

where $P(O|\Pi_i)$ is the probability of the observed state O given the latent state, which is the detection probability of that state, as estimated by the model. $P(\Pi_i)$ is the probability of state Π_i and is the transition probability from the previous latent state, as estimated by the model. $P(O)$ is the probability of the observed state, and is the sum of observing O given all possible latent states, i.e., $\sum_k P(O|\Pi_k)P(\Pi_k)$. In addition, the probability of a dead individual at a given time step was set to zero when the individual was subsequently detected alive. The process was repeated for each of the 6 000 MCMC samples from the model, and the resulting population structure in 2021—and its uncertainty— was taken as the initial population for the simulations. Pre-breeders and adults outside the study area were not included, to simulate only the population inside the study area and the juveniles that fledged from there.

The population size from the simulations was scaled up by the ratio of the total number of breeding pairs on the island to the number of breeding pairs inside the study area. The total number of breeding pairs was estimated from extensive surveys of the whole island in 1994, 1995, and 1996. The scaling of the studied population size to the whole island, therefore, assumes that the ratio did not change over time. The proportion of the number of breeding pairs that were inside the study area was estimated to be 2.7332% averaged across the three censuses (Elliott & Walker 2020), and the inverse of this value (36.58715) was used to scale up the simulation population size to the whole island.

The population simulations consisted of predicting the fate of each individual in the initial 2021 population, and of new fledglings produced each year, every year for 30 years, based on the demographic parameters estimated in the model. For each simulated year, an actual year between 2008 and 2020 was first drawn randomly to represent the interannual variability estimated in the model, while considering only the most recent years. The drawn year defined the value of survival rates and breeding success. Surviving individuals were drawn following a Bernoulli process with a probability equal to the survival rate of the drawn year and of the individual class (juvenile, pre-breeder, adult female, or adult male). Juveniles and pre-breeders either remained in their age class or moved to the next one depending on the age-specific transition probabilities. Adults breeding that year were then drawn according to the probability of breeding, depending on whether they bred successfully (or not) the previous year. The success of breeding adults was then drawn randomly from the probability of success of that year. Among successful breeders, the number of fledglings produced was taken as the minimum number of female or male adults, and new individuals of age 0 were created, with a sex assigned randomly with a probability of 0.5. This process was then repeated iteratively for the 30 simulated years, and for each iteration of the MCMC methods.

In the online tool, scenarios are specified in terms of direct impacts, affecting specific demographic parameters. Threats can impact the annual survival rate of juveniles, pre-breeders, adult males, and adult females separately, or can also impact breeding probability or breeding success. The threats can be defined as being either already present, in which case the impact is removed from the population in the simulations, or potential, with the impact added to the population. For example, to assess the potential effect of introducing new mitigation measures in fisheries, the impact would need to be specified as already present, and the incidental mortalities would be removed from the population in the simulations.

Impacts may be specified as an absolute change in the demographic parameter, or as a number of individuals for survival rates. When using individuals, the impact is converted to the absolute change in survival rate, Δ, based on the total number of individuals in the affected category:

$$\Delta = S' - S = 1 - \frac{(1-\Phi)N - I}{N} - \Phi, \tag{21}$$

where S' is the new survival rate, Φ the survival rate of the population category (juvenile, pre-breeder, adult female, or adult male), N the scaled-up number of individuals in the category, and I the number of mortalities caused by the threat. The conversion of impacts from individuals to a change in demographic rates assumes that the impact of threats is consistently proportional to the population size.

Multiple threats and impacts may be specified for a given scenario. In that case, the overall change in demographic parameters is calculated by summing the absolute changes across threats and impacts within each demographic parameter.

Upon completion of the simulations, the mean and 95% credible interval of the population size, of the number of annual breeding pairs, and population mean annual growth rate, and the mean population structure are calculated and reported, in tables and figures.

For illustration purposes, two hypothetical scenarios were simulate here, representing two existing threats; each threat resulted in the death of 500 individuals, but only of juveniles in one scenario, and only of adults in the other scenario (male and female).

3. RESULTS

3.1 Model parameters

The MCMC traces indicated that the model converged reasonably well, as the four chains were well mixed and did not show significant autocorrelation (see Appendix B for the MCMC traces and values of each demographic parameter estimated by the model). One exception was the parameter related to the detection probability, which converged but showed marked autocorrelation. (This autocorrelation will be corrected during a longer and thinned fitting of the final model, upon finalising this report.)

The estimated adult annual survival rate between 1994 and 2020 showed changes over time (Figure 1). Before 2005, the estimated survival rate was similar between sexes, with an annual mean of 0.947 (95% c.i.: 0.914 – 0.973). From 2005, however, estimated female survival declined to a mean of 0.882 (95% c.i.: 0.814 – 0.94); female survival was lowest in 2013, estimated at 0.821 (95% c.i.: 0.752 – 0.883). In contrast, male survival only slightly declined to a mean of 0.927 (95% c.i.: 0.887 – 0.961), with a minimum around 0.90 in 2007.

The estimated survival in the the three most recent years (2018 to 2020) suggested a possible increase to levels similar to estimates before 2004, with female adult survival reaching 0.929 (95% c.i.: 0.861 – 0.976) in 2020, and adult male survival at 0.971 (95% c.i.: 0.943 – 0.991).

The annual survival rate of juveniles and pre-breeders, assumed to be constant among

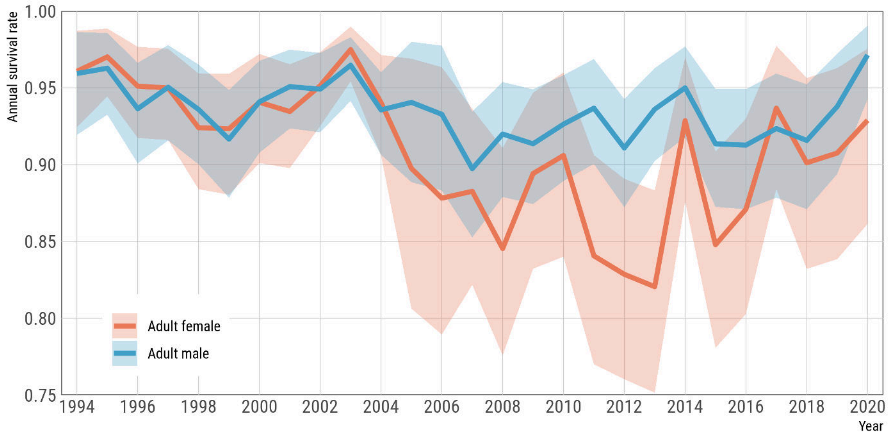

Figure 1: Adult annual survival for female and male Antipodean albatross between 1994 and 2020, estimated from the demographic model. Lines indicate the mean, shading the 95% credible interval.

years, was estimated at 0.879 (95% c.i.: 0.869 – 0.888) and 0.922 (95% c.i.: 0.913 – 0.931), respectively.

The change of adult survival rates over time was significant even though the interannual variability in the probability of detection was controlled in the model. The detection probability also showed a decrease over time, i.e., after 2006 (Figure 2).

despite controlling in the model for the inter-annual variability in the probability of detection, which also showed an overall decrease after 2006 (Figure 2).

The interannual change in detectability, applied to all individual types present on the island, was related to both the timing and length of the field seasons on the island (Figure 3). Estimates of detectability were highest when the field season started early (early December) and when the survey effort was high, both in the number of days with recorded field observations, and in the total number of recorded observations in the season.

Amongst the years with the lowest detectability, 1995 and 2020 were characterised by a low number of field days and observations, and started late in the season (mid-February and mid-March, respectively). In contrast, the highest estimated detectability was in 2003, when the field season was both the second earliest (mid-December) and the second longest (60 days of observations).

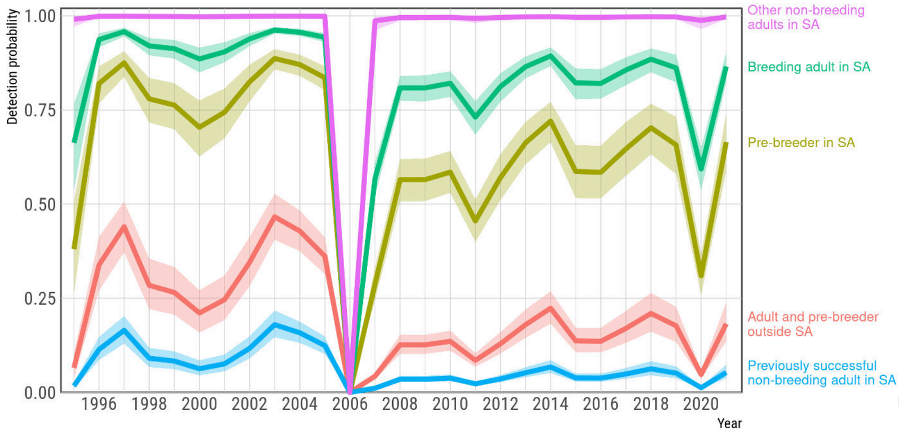

Figure 2: Detection probability of individuals inside the study area (SA) for breeding adults, non-breeders that were were previously successful breeders, other non-breeders, and pre-breeders, and for adults and pre-breeders combined outside the study area. Lines indicate the mean, shading the 95% credible interval.

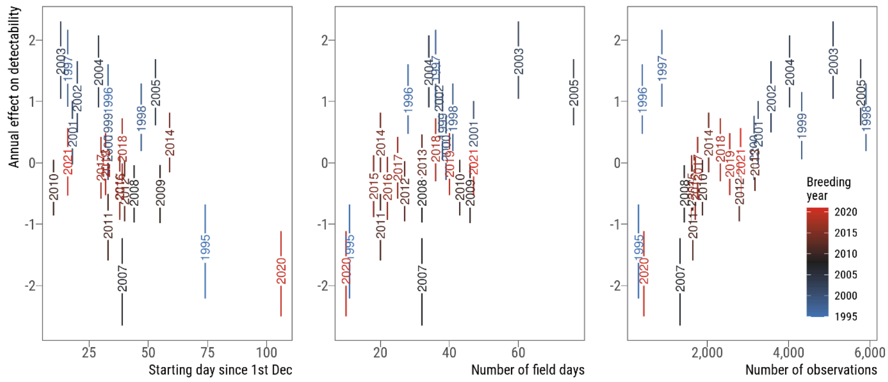

Figure 3: Relation between the interannual variability of the probability of detection and the timing and effort of population surveys. The timing of surveys was measured here as the number of days between the 1 December preceding the breeding season and the first day of recorded observations. Observation effort is in the number of days with observations, and the total number of observations recorded during the breeding season. The annual effect on detectability is shown as the 95% credible interval of the annual random effect as estimated in the model, and the label showing the year of the field season is centred on the mean estimate.

The estimated probability of detection varied significantly between the types of individuals considered in the model (Table 1 and Figure 2). This probability was around 5.2% for non-breeding adults that were successful breeders the previous years, 18.0% for adults and pre-breeders outside the study area, 66.1% for pre-breeders inside the study area, 86.4% for adults breeding inside the study area, and 99.7% for non-breeding adults that were not successful breeders in the previous year. Additionally, the detectability was estimated close to zero for both juveniles and dead individuals, with a mean of 0.019% (95% c.i.: 0% – 0.073%) and 0.083% (95% c.i.: 0.054% – 0.118%), respectively.

Table 1: Mean estimates (and credible interval, c.i.) of the probability of detection among the different individual types in the Antipodean albatross population considered in the demographic model (SA, study area).

Type	Mean	95% c.i.
Breeding adult in SA	0.864	0.816 – 0.900
Previously successful non-breeding adult in SA	0.052	0.036 – 0.072
Other non-breeding adults in SA	0.997	0.992 – 1.000
Pre-breeder in SA	0.661	0.575 – 0.736
Adult and pre-breeder outside SA	0.180	0.132 – 0.234

The probability of breeding was estimated in the model, and assumed to be constant among years. For adults that were failed breeders the previous year, the probability of breeding was estimated at 70.5% (95% c.i.: 68.6% – 72.3%). The probability was significantly lower for other individuals that were previously non-breeders, at 64.1% (95% c.i.: 62.8% – 65.4%). For adults that were successful breeders in the previous year, this probability was zero.

As for survival, breeding success was also allowed to vary among years in the model. Modelled as the probability that a nest successfully produces a fledgling, breeding success also declined between the period 1994–2004 and 2005–2021 (Figure 4). Prior to 2005, the mean breeding success was estimated at 72.4% (95% c.i.: 65.8% – 78.6%), but at 63.7% (95% c.i.: 53.4% – 73%) after 2005.

To take into account bird movements in and out of the study area for the estimation of survival rates, the probability of individuals that were inside the study area leaving the area, and conversely the probability of individuals that were outside the study area returning to it, were estimated for females and males independently, and assumed to be constant among years. These probabilities suggest that females are less faithful to their area than males, as females had a 9% (95% c.i.: 8.1% – 10%) probability of leaving the study area, compared with 4% (95% c.i.: 3.5% – 4.6%) for males. Similarly, females had an estimated probability of 17.7% (95% c.i.: 15.2% – 20.3%) to return to the colony after

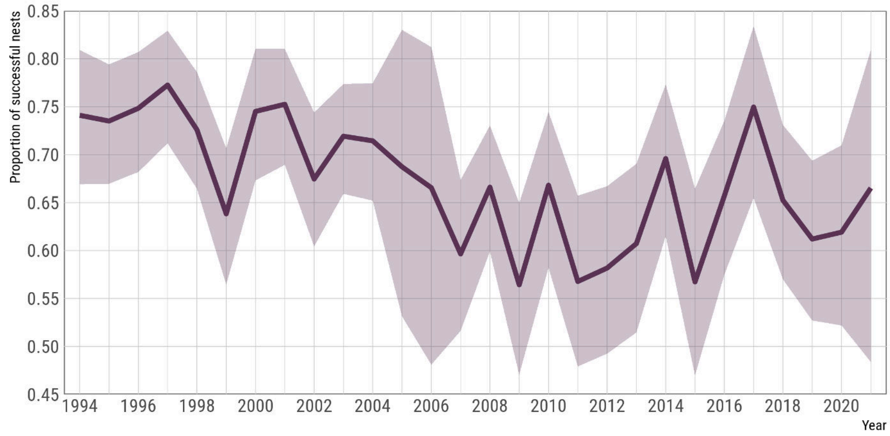

Figure 4: Breeding success by year for Antipodean albatross between 1994 and 2021, measured as the proportion of nests producing a fledgling. Line indicates the mean, shading the 95% credible interval.

leaving it, compared with 25.4% (95% c.i.: 21.9% – 29.1%) for males.

The ages at first return and at first breeding were also estimated in the model (Figure 5). The age at first return varied between 3 and 9 years, with an average at 6.26 years. The minimum age at first breeding was 7 years, and by age 13, half of the individuals had bred at least once, although some individuals did not breed at all.

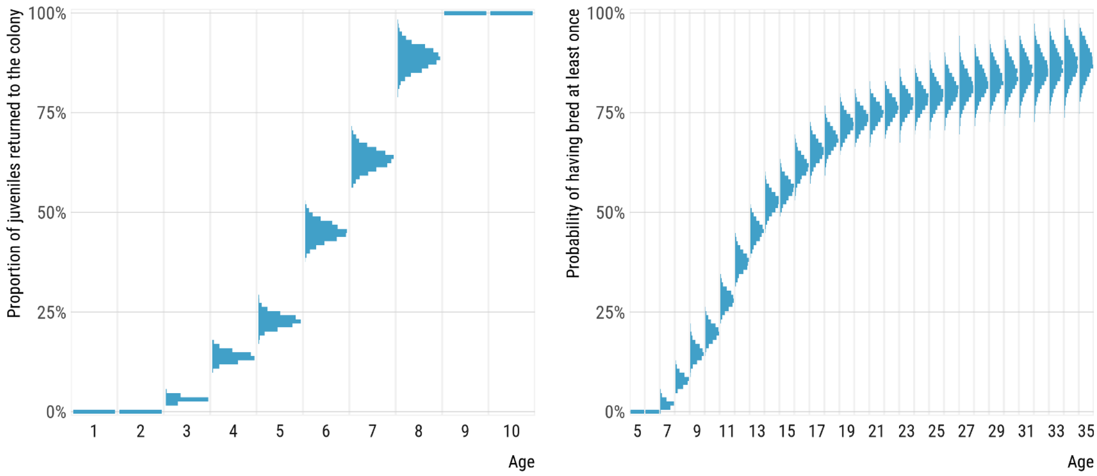

Figure 5: Proportion of individuals that returned to the colony (left) and proportion of individuals that bred at least once as function of age (right). For each age, a histogram of the Markov chain Monte Carlo values is shown as estimated by the model.

3.2 Online simulation tool

Based on the demographic parameters obtained from the model, an online application was developed to simulate the population dynamics of Antipodean albatross under different scenarios (see a screenshot of the online simulation tool in Figure 6).

The structure of the population in 2021 was used for the initialisation of the simulations, and was obtained from drawing iteratively the latent state of each individual in the study area each year when the state was unknown (examples of the predictions of individual state are shown in Figure 7).

The number of number of breeding pairs inside the study area from on-site surveys was similar to the estimate derived from the model estimates (Figure 8). Nevertheless, the model estimate was higher overall. This difference was due to the model estimate including the individuals that are not detected during surveys.

The population in 2021 used to initialise the simulations was estimated inside the study area at 90 (95% c.i.: 81 – 100) breeding pairs, and 762 (95% c.i.: 726 – 801) total individuals. Scaling up to the entire island, these estimates represent a total of 3,292 (95% c.i.: 2,964 – 3,659) breeding pairs and 27,893 (95% c.i.: 26,562 – 29,306) total individuals.

On average, the population consisted of 15.7% juvenile, 21.3% pre-breeders, 37.5% non-breeding adults, 17% successful breeding adults, and 8.6% unsuccessful breeding adults.

In the current context, i.e., without specifying any management scenario, simulations predicted a population decline of 4.84% (95% c.i.: 3.65% – 6.07%) with the total annual number of breeding pairs in the study area decreasing from 90 (95% c.i.: 81 – 100) to 11 (95% c.i.: 4 – 21) after 30 years ("Current context" in Figure 9). Scaling up the study area population to the entire island, this estimate corresponded to a decline from 3,292 (95% c.i.: 2,964 – 3,659) breeding pairs to 401 (95% c.i.: 146 – 768), or for the whole population, from 27,893 (95% c.i.: 26,562 – 29,306) birds to 6,412 (95% c.i.: 4,244 – 9,183).

When simulating a hypothetical scenario of mitigating an existing threat causing the death of 500 juveniles, the rate of decline decreased to 3.3% (95% c.i.: 2.1% – 4.6%); when the mortalities only affected adults, the rate further decreased to 2.7% (95% c.i.: 1.5% –

Figure 6: Screenshot of the online application tool to run predictions of the Antipodean albatross population in the future under different scenarios.

4%) (Figure 9).

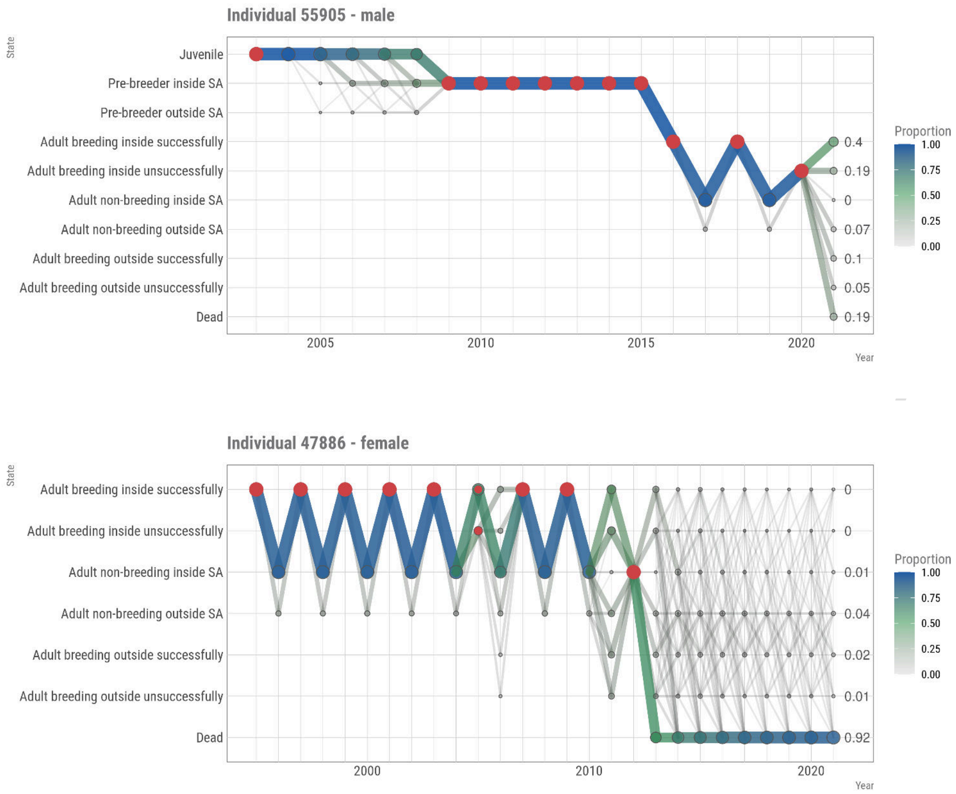

Figure 7: Examples of drawing the latent state of individuals from their observed state. Red dots represent the latent states that are possible given the observed state of an individual that was detected. The size and colour of segments indicate the probability of transition between two successive states. Numbers indicate the probability of each state in 2021, used to draw the initial population structure for population projections.

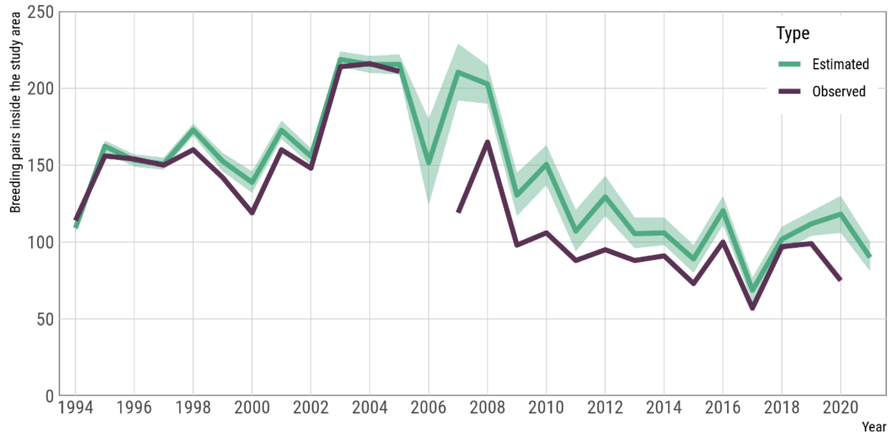

Figure 8: Comparison of the annual number of breeding pairs when recorded during field surveys (Observed) and when estimated from the model (Estimated). Lines indicate the mean, shading the 95% credible interval for the estimate.

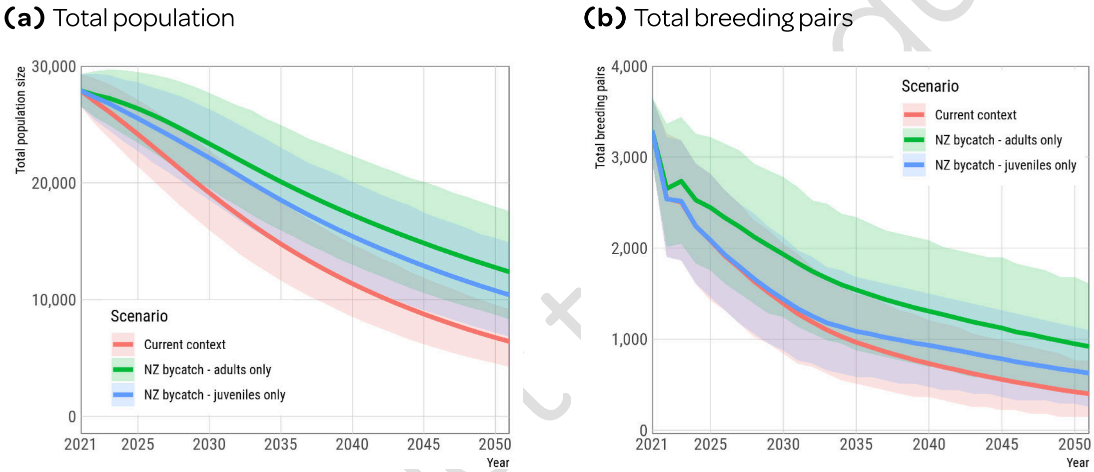

Figure 9: Simulation of the population size (a) and of the number of annual breeding pairs (b) of Antipodean albatross over the next 30 years on Antipodes Island. The simulation is based on the demographic parameters estimated in the model, only keeping the time-varying values between 2008 and 2020. The mean and 95% credible interval are shown.

4. DISCUSSION

The aim of this project was to provide an online simulation tool for predicting the outcome of management strategies on the demography of Antipodean albatross. As for any model, the accuracy of the prediction depends on the input field data, the complexity of the factors affecting the demography, and the change over time in the threats to the species.

Although movements in and out of the study area were included in the model, any permanent emigration from the study area was more likely to be considered as local mortality, and may underestimate annual survival rate. The area around the study site has been visited regularly and sightings recorded there were used in the model to estimate the rate of movements between areas. It is a relatively small area compared with the rest of the island; some individuals may not be seen again once they relocate permanently, making their emigration indistinguishable from death. Nevertheless, the observations of the researchers when travelling across the island suggest that permanent emigration by a significant number of individuals is unlikely (G. Elliott, pers. comm.).

The current model specification was designed to provide a basis for the simulations, and compromises were made to balance realism and simplicity. For example, a number of parameters were not dependent on years, such as the probability of breeding or the survival rate of pre-breeders, and the model presented here may not be the closest representation of reality. For this reason, the model results and the absolute projections into the future need to be considered with caution. Nevertheless, it should be sufficient to compare the relative impact of alternative management strategies. (Slight changes to the model may be applied upon finalisation of this report.)

The recent increase in survival rates since 2018 may be a probabilistic coincidence, but could also indicate an alleviation of the threats affecting females predominantly. For example, fisheries may operate in different areas over time, or the areas where individuals forage may also vary, resulting in a change in the overlap between the species and fishery threats. The next few years of field data will inform whether this trend continues.

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I am sincerely thankful to Graeme Elliott and Kath Walker for providing us with the data they have tenaciously collected over decades, and for sharing their experience of the species and field work.

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Data preparation and statistical analyses were carried out using R (including the libraries data.table and rstan) and Stan, writing scripts using Emacs, containerised using Docker, and this document was produced using LaTeX. We are extremely grateful to the many people who contribute to these key open source software projects and make them available.

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APPENDIX A STAN MODEL CODE

```
functions{

  matrix trans_probs(int nstates, real s_ad, real s_prebr, real s_juv,
                     real p_mv_out, real p_mv_in, int succ, vector p_breed,
                     real p_rec, real p_bead, real p_succ) {

    /** TRANSITIONS and SURVIVAL **/

    // 1: adults breeding inside SA
    // 2: adults breeding outside SA
    // 3: adults non-breeding inside SA
    // 4: adults non-breeding outside SA
    // 5: pre-breeders inside SA
    // 6: pre-breeders outside SA
    // 7: juvs
    // 8: deads

    matrix[nstates, nstates] tmat;

    //* ADULTS PREVIOUSLY BREEDING WITHIN STUDY AREA *//
    // re-breeding in SA (SA = study area)
    tmat[1, 1] = succ == 2 ?
      0 :
      (succ == 1 ?
       p_breed[1] * s_ad * (1-p_mv_out) :
       (1-p_succ) * p_breed[1] * s_ad * (1-p_mv_out));
    // re-breeding outside SA
    tmat[1, 2] = succ == 2 ?
      0 :
      (succ == 1 ?
       p_breed[1] * s_ad *    p_mv_out  :
       (1-p_succ) * p_breed[1] * s_ad *    p_mv_out);
    // non-breeding in SA
    tmat[1, 3] = succ == 2 ?
      s_ad * (1-p_mv_out) :
      (succ == 1 ?
       (1-p_breed[1]) * s_ad * (1-p_mv_out) :
       (1-p_succ) * (1-p_breed[1]) * s_ad * (1-p_mv_out) +
       p_succ * s_ad * (1-p_mv_out));
    // non-breeding outside SA
    tmat[1, 4] = succ == 2 ?
      s_ad * p_mv_out :
      (succ == 1 ?
       (1-p_breed[1]) * s_ad * p_mv_out :
       (1-p_succ) * (1-p_breed[1]) * s_ad * p_mv_out +
       p_succ * s_ad * p_mv_out);
    tmat[1, 5] = 0;              // pre-breeders inside SA
    tmat[1, 6] = 0;              // pre-breeders outside SA
    tmat[1, 7] = 0;              // juvs
    tmat[1, 8] = 1-s_ad;         // dead

    //* ADULTS PREVIOUSLY BREEDING OUTSIDE STUDY AREA *//
    // re-breeding in SA (SA = study area)
    tmat[2, 1] = succ == 2 ?
      0 :
      (succ == 1 ?
       p_breed[1] * s_ad * p_mv_in :
       (1-p_succ) * p_breed[1] * s_ad * p_mv_in);
    // re-breeding outside SA
    tmat[2, 2] = succ == 2 ?
      0 :
      (succ == 1 ?
       p_breed[1] * s_ad * (1-p_mv_in) :
       (1-p_succ) * p_breed[1] * s_ad * (1-p_mv_in));
    // non-breeding in SA
    tmat[2, 3] = succ == 2 ?
      s_ad * p_mv_in :
      (succ == 1 ?
       (1-p_breed[1]) * s_ad * p_mv_in :
      (1-p_succ) * (1-p_breed[1]) * s_ad * p_mv_in  +  p_succ * s_ad * p_mv_in);
    // non-breeding outside SA
    tmat[2, 4] = succ == 2 ?
      s_ad * (1-p_mv_in) :
      (succ == 1 ?
       (1-p_breed[1]) * s_ad * (1-p_mv_in) :
       (1-p_succ) * (1-p_breed[1]) * s_ad * (1-p_mv_in)  +  p_succ * s_ad * (1-p_mv_in));
    tmat[2, 5] = 0;              // pre-breeders inside SA
    tmat[2, 6] = 0;              // pre-breeders outside SA
    tmat[2, 7] = 0;              // juvs
    tmat[2, 8] = 1-s_ad;         // dead

    //* ADULTS PREVIOUSLY NOT BREEDING WITHIN STUDY AREA *//
    tmat[3, 1] =    p_breed[2]  * s_ad * (1-p_mv_out);  // breeding in SA (SA = study area)
    tmat[3, 2] =    p_breed[2]  * s_ad *    p_mv_out;   // breeding outside SA
    tmat[3, 3] = (1-p_breed[2]) * s_ad * (1-p_mv_out);  // non-breeding in SA
    tmat[3, 4] = (1-p_breed[2]) * s_ad *    p_mv_out;   // non-breeding outside SA
    tmat[3, 5] = 0;                                     // pre-breeders inside SA
    tmat[3, 6] = 0;                                     // pre-breeders outside SA
    tmat[3, 7] = 0;                                     // juvs
```

```
    tmat[3, 8] = 1-s_ad;                              // dead

    //* ADULTS PREVIOUSLY NOT BREEDING OUTSIDE THE STUDY AREA *//
    tmat[4, 1] =    p_breed[2]  * s_ad *    p_mv_in;   // breeding in SA (SA = study area)
    tmat[4, 2] =    p_breed[2]  * s_ad * (1-p_mv_in);  // breeding outside SA
    tmat[4, 3] = (1-p_breed[2]) * s_ad *    p_mv_in;   // non-breeding in SA
    tmat[4, 4] = (1-p_breed[2]) * s_ad * (1-p_mv_in);  // non-breeding outside SA
    tmat[4, 5] = 0;                                   // pre-breeders inside SA
    tmat[4, 6] = 0;                                   // pre-breeders outside SA
    tmat[4, 7] = 0;                                   // juvs
    tmat[4, 8] = 1-s_ad;                              // dead

    //* PRE-BREEDERS INSIDE THE STUDY AREA *//
    tmat[5, 1] = s_prebr * p_bead * (1-p_mv_out);      // breeding in SA (SA = study area)
    tmat[5, 2] = s_prebr * p_bead *    p_mv_out;       // breeding outside SA
    tmat[5, 3] = 0;                                   // non-breeding in SA
    tmat[5, 4] = 0;                                   // non-breeding outside SA
    tmat[5, 5] = s_prebr * (1-p_bead) * (1-p_mv_out);  // pre-breeders inside SA
    tmat[5, 6] = s_prebr * (1-p_bead) *    p_mv_out;   // pre-breeders outside SA
    tmat[5, 7] = 0;                                   // juvs
    tmat[5, 8] = 1-s_prebr;                           // dead

    //* PRE-BREEDERS OUTSIDE THE STUDY AREA *//
    tmat[6, 1] = s_prebr * p_bead *    p_mv_in;        // breeding in SA (SA = study area)
    tmat[6, 2] = s_prebr * p_bead * (1-p_mv_in);       // breeding outside SA
    tmat[6, 3] = 0;                                   // non-breeding in SA
    tmat[6, 4] = 0;                                   // non-breeding outside SA
    tmat[6, 5] = s_prebr * (1-p_bead) *    p_mv_in;    // pre-breeders inside SA
    tmat[6, 6] = s_prebr * (1-p_bead) * (1-p_mv_in);   // pre-breeders outside SA
    tmat[6, 7] = 0;                                   // juvs
    tmat[6, 8] = 1-s_prebr;                           // dead

    //* JUVENILES *//
    tmat[7, 1] = 0;                           // breeding in SA (SA = study area)
    tmat[7, 2] = 0;                           // breeding outside SA
    tmat[7, 3] = 0;                           // non-breeding in SA
    tmat[7, 4] = 0;                           // non-breeding outside SA
    tmat[7, 5] = s_juv * p_rec * (1-p_mv_out); // pre-breeders inside SA
    tmat[7, 6] = s_juv * p_rec *    p_mv_out;  // pre-breeders outside SA
    tmat[7, 7] = s_juv * (1-p_rec);           // juvs
    tmat[7, 8] = 1-s_juv;                     // dead

    //* DEADS *//
    tmat[8, 1] = 0;     // breeding in SA (SA = study area)
    tmat[8, 2] = 0;     // breeding outside SA
    tmat[8, 3] = 0;     // non-breeding in SA
    tmat[8, 4] = 0;     // non-breeding outside SA
    tmat[8, 5] = 0;     // pre-breeders inside SA
    tmat[8, 6] = 0;     // pre-breeders outside SA
    tmat[8, 7] = 0;     // juvs
    tmat[8, 8] = 1;     // dead

    return tmat;
  }


  matrix obs_probs(int n_obs_states, real[] p_obs, real p_detect_juv, real p_detect_dead,
                   real p_female, real p_succ, int succ, int no_visit) {

    /** OBSERVED STATES **/

    // 1: adults breeding in SA
    // 2: adults non-breeding in SA
    // 3: adults outside SA
    // 4: pre-breeders inside SA
    // 5: pre-breeders outside SA
    // 6: juvs
    // 7: dead
    // 8: not seen

    matrix[n_obs_states, n_obs_states] pmat;

    //* ADULTS BREEDING WITHIN STUDY AREA *//
    pmat[1, 1] = no_visit == 1 ? 0 : p_obs[1];  // ad breeding in SA (SA = study area)
    pmat[1, 2] = 0;                           // ad non-breeding in SA
    pmat[1, 3] = 0;                           // ad outside SA
    pmat[1, 4] = 0;                           // pre-breeders inside SA
    pmat[1, 5] = 0;                           // pre-breeders outside SA
    pmat[1, 6] = 0;                           // juvs
    pmat[1, 7] = 0;                           // dead
    pmat[1, 8] = 1 - pmat[1, 1];              // not seen

    //* ADULTS BREEDING OUTSIDE STUDY AREA *//
    pmat[2, 1] = 0;                           // ad breeding in SA (SA = study area)
    pmat[2, 2] = 0;                           // ad non-breeding in SA
    pmat[2, 3] = no_visit == 1 ? 0 : p_obs[5];  // ad outside SA
    pmat[2, 4] = 0;                           // pre-breeders inside SA
    pmat[2, 5] = 0;                           // pre-breeders outside SA
    pmat[2, 6] = 0;                           // juvs
    pmat[2, 7] = 0;                           // dead
    pmat[2, 8] = 1 - pmat[2, 3];              // not seen
```

```
    //* ADULTS NON-BREEDING INSIDE STUDY AREA *//
    pmat[3, 1] = 0;                      // ad breeding in SA (SA = study area)
    pmat[3, 2] = no_visit == 1 ?         // ad non-breeding in SA
      0 :
      (succ == 2 ?
       p_obs[2] :
       (succ == 1 ?
        p_obs[3] :
        p_succ * p_obs[2] + (1-p_succ) * p_obs[3]));
    pmat[3, 3] = 0;                      // ad outside SA
    pmat[3, 4] = 0;                      // pre-breeders inside SA
    pmat[3, 5] = 0;                      // pre-breeders outside SA
    pmat[3, 6] = 0;                      // juvs
    pmat[3, 7] = 0;                      // dead
    pmat[3, 8] = 1 - pmat[3, 2];         // not seen

    //* ADULTS NON-BREEDING OUTSIDE STUDY AREA *//
    pmat[4, 1] = 0;                              // ad breeding in SA (SA = study area)
    pmat[4, 2] = 0;                              // ad non-breeding in SA
    pmat[4, 3] = no_visit == 1 ? 0 : p_obs[5];  // ad outside SA
    pmat[4, 4] = 0;                              // pre-breeders inside SA
    pmat[4, 5] = 0;                              // pre-breeders outside SA
    pmat[4, 6] = 0;                              // juvs
    pmat[4, 7] = 0;                              // dead
    pmat[4, 8] = 1 - pmat[4, 3];                 // not seen

    //* PRE-BREEDERS INSIDE STUDY AREA *//
    pmat[5, 1] = 0;                              // ad breeding in SA (SA = study area)
    pmat[5, 2] = 0;                              // ad non-breeding in SA
    pmat[5, 3] = 0;                              // ad outside SA
    pmat[5, 4] = no_visit == 1 ? 0 : p_obs[4];  // pre-breeders inside SA
    pmat[5, 5] = 0;                              // pre-breeders outside SA
    pmat[5, 6] = 0;                              // juvs
    pmat[5, 7] = 0;                              // dead
    pmat[5, 8] = 1 - pmat[5, 4];                 // not seen

    //* PRE-BREEDERS OUTSIDE STUDY AREA *//
    pmat[6, 1] = 0;                              // ad breeding in SA (SA = study area)
    pmat[6, 2] = 0;                              // ad non-breeding in SA
    pmat[6, 3] = 0;                              // ad outside SA
    pmat[6, 4] = 0;                              // pre-breeders inside SA
    pmat[6, 5] = no_visit == 1 ? 0 : p_obs[5];  // pre-breeders outside SA
    pmat[6, 6] = 0;                              // juvs
    pmat[6, 7] = 0;                              // dead
    pmat[6, 8] = 1 - pmat[6, 5];                 // not seen

    //* JUVENILES *//
    pmat[7, 1] = 0;                                      // ad breeding in SA (SA = study area)
    pmat[7, 2] = 0;                                      // ad non-breeding in SA
    pmat[7, 3] = 0;                                      // ad outside SA
    pmat[7, 4] = 0;                                      // pre-breeders inside SA
    pmat[7, 5] = 0;                                      // pre-breeders outside SA
    pmat[7, 6] = no_visit == 1 ? 0 : p_detect_juv;      // juvs
    pmat[7, 7] = 0;                                      // dead
    pmat[7, 8] = 1 - pmat[7, 6];                         // not seen

    //* DEADS *//
    pmat[8, 1] = 0;                                      // ad breeding in SA (SA = study area)
    pmat[8, 2] = 0;                                      // ad non-breeding in SA
    pmat[8, 3] = 0;                                      // ad outside SA
    pmat[8, 4] = 0;                                      // pre-breeders inside SA
    pmat[8, 5] = 0;                                      // pre-breeders outside SA
    pmat[8, 6] = 0;                                      // juvs
    pmat[8, 7] = no_visit == 1 ? 0 : p_detect_dead;     // dead
    pmat[8, 8] = 1 - pmat[8, 7];                         // not seen

    return pmat;
  }


  real log_sum_one_indiv (int N_STATES, int sex, int[] age, int MAX_T, int first_cap, int last_cap,
                          int[] c_hist, real[,] s_ad, real s_prebr, real s_juv, real[] p_moveout,
                          real[] p_movein, int[] b_success, vector p_breed, vector p_recruit,
                          vector p_beadult, real[] p_success, int N_STATES_P, real[,] p_obs,
                          real p_detect_juv, real p_detect_dead, real p_female, int[] NO_VISIT,
                          int first_state) {

    matrix[N_STATES, N_STATES] tmat;
    matrix[N_STATES_P, N_STATES_P] pmat;
    vector[N_STATES] pz[MAX_T];
    real temp[N_STATES];
    real lsum;

    for (j in 1:N_STATES) {
      pz[first_cap, j] = (j == first_state);
    }
    for (t in (first_cap+1):last_cap) {
      tmat = trans_probs(N_STATES, s_ad[sex+1, t-1], s_prebr, s_juv,
                         p_moveout[sex+1], p_movein[sex+1], b_success[t-1],
                         p_breed, p_recruit[age[t]], p_beadult[age[t]],
```

```
                          p_success[t-1]);
      pmat = obs_probs(N_STATES_P, p_obs[t-1], p_detect_juv, p_detect_dead, p_female,
                        p_success[t-1], b_success[t-1], NO_VISIT[t]);
      for (i in 1:N_STATES) {
        for (j in 1:N_STATES) {
          temp[j] = pz[t-1, j] * tmat[j, i] * pmat[i, c_hist[t]];
        }
        pz[t, i] = sum(temp);
      }
    }

    lsum = log(sum(pz[last_cap]));

    return lsum;

  }


  real calc_log_sum_multi (int[] INDS, int start, int end, int N_STATES, int[] SEX, int[,] AGE,
                            int MAX_T, int[] FIRST_CAP, int[] LAST_CAP, int[,] C_HIST,
                            real[,] s_ad, real s_prebr, real s_juv,
                            real[] p_moveout, real[] p_movein, int[,] B_SUCCESS, vector p_breed,
                            vector p_recruit, vector p_beadult, real[] p_success,
                            int N_STATES_P, real[,] p_obs, real p_detect_juv, real p_detect_dead, real p_female,
                            int[] NO_VISIT, int[] FIRST_STATE) {
    real lsum;

    lsum = 0.0;
    for (ind in start:end) {

      lsum += log_sum_one_indiv(N_STATES, SEX[ind], AGE[ind], MAX_T, FIRST_CAP[ind], LAST_CAP[ind], C_HIST[ind],
                                 s_ad, s_prebr, s_juv, p_moveout, p_movein,
                                 B_SUCCESS[ind], p_breed,
                                 p_recruit, p_beadult, p_success,
                                 N_STATES_P, p_obs, p_detect_juv, p_detect_dead, p_female,
                                 NO_VISIT, FIRST_STATE[ind]); //, ind);
    }

    return lsum;

  }

}

data {

  int<lower=1> N_INDS;
  int<lower=1> INDS [N_INDS];
  int<lower=1> FIRST_STATE [N_INDS];

  int<lower=0, upper=2> SEX [N_INDS];
  int<lower=1> N_SEXED;
  int<lower=0, upper=1> IS_FEMALE [N_SEXED];

  int<lower=1> N_NESTS;
  int<lower=0, upper=1> NEST_SUCCESS [N_NESTS];
  int<lower=1> NEST_YEAR [N_NESTS];

  int<lower=1> FIRST_CAP [N_INDS];
  int<lower=1> LAST_CAP  [N_INDS];

  int<lower=1> MAX_T;
  int<lower=1> MAX_AGE;
  int<lower=1> AGE[N_INDS, MAX_T];

  int<lower=1, upper=MAX_AGE> MIN_R_AGE;
  int<lower=MIN_R_AGE, upper=MAX_AGE> MAX_R_AGE;
  int<lower=MIN_R_AGE, upper=MAX_AGE> MIN_B_AGE;
  int<lower=MIN_B_AGE, upper=MAX_AGE> MIN_B_AGE2;

  int<lower=0, upper=1> NO_VISIT[MAX_T];

  int<lower=1> N_STATES;
  int<lower=1> N_STATES_P;
  int<lower=1> N_PDETECTS;
  int<lower=1, upper=N_STATES_P> C_HIST[N_INDS, MAX_T];

  int<lower=0, upper=2> B_SUCCESS[N_INDS, MAX_T];

}


transformed data {
  int<lower=1> grainsize=1;
}


parameters{

  real<lower=0, upper=1> p_female;
```

```
  real<lower=0, upper=1> p_rec [MAX_R_AGE - MIN_R_AGE + 1];

  real<lower=0, upper=1> p_br [MIN_B_AGE2 - MIN_B_AGE];
  real<lower=0, upper=1> p_br_post;

  vector<lower=0, upper=1>[2] p_breed; // 1: previously unsucessful breeders; 2: other non-breeders

  real<lower=0> sigma_re_bsucc;
  real bsucc_lg_re [MAX_T];
  real bsucc_lg_mean;

  real<lower=0, upper=1> s_prebr;
  real<lower=0, upper=1> s_juv;

  /* Random effect on recruitment */
  real<lower=0> sigma_re_rec;
  real rec_lg_re [MAX_R_AGE - MIN_R_AGE + 1];
  real rec_lg_mean;

  /* Random effect on becoming adult */
  real<lower=0> sigma_re_bead;
  real bead_lg_re [MIN_B_AGE2 - MIN_B_AGE];
  real bead_lg_mean;

  /* Random effect on adult survival */
  real<lower=0> sigma_re_ad_s;
  real surv_ad_lg_re [2, MAX_T-1];
  real surv_ad_lg_mean [2];

  /* Random effect on detectability */
  real<lower=0> sigma_re_p;
  real p_detect_lg_re [MAX_T-1];
  real p_detect_lg_mean [N_PDETECTS];
  real<lower=0, upper=1> p_detect_juv;
  real<lower=0, upper=1> p_detect_dead;

  real<lower=0, upper=1> p_leave[2];
  real<lower=0, upper=1> p_back[2];

}


transformed parameters {

  vector<lower=0, upper=1>[MAX_AGE] p_recruit;
  vector<lower=0, upper=1>[MAX_AGE] p_beadult;

  real<lower=0, upper=1> s_adult [2, MAX_T-1];
  real<lower=0, upper=1> s_ad[3, MAX_T-1];

  real<lower=0, upper=1> p_detect [N_PDETECTS, MAX_T-1]; // 1: breeding ad (inside sa); 2: non-breeding ad previously
     successful (inside sa); 3: other non-breeders (inside sa); 4: prebr inside SA; 5: ad or prebr outside SA

  real<lower=0, upper=1> p_success [MAX_T];

  real<lower=0, upper=1> p_moveout [3];
  real<lower=0, upper=1> p_movein [3];

  real<lower=0, upper=1> p_obs [MAX_T-1, N_PDETECTS];

  /* Juvs becoming pre-breeders (recruitment to the colony) */
  for (a in 1:(MIN_R_AGE-1)) {
    p_recruit[a] = 0;
  }
  for (a in MIN_R_AGE:MAX_R_AGE) {
    p_recruit[a] = inv_logit(rec_lg_mean + rec_lg_re[a - MIN_R_AGE + 1] * sigma_re_rec);
  }
  for (a in (MAX_R_AGE+1):MAX_AGE) {
    p_recruit[a] = 1;
  }

  /* Pre-Breeders becoming adults (start breeding) */
  for (a in 1:(MIN_B_AGE-1)) {
    p_beadult[a] = 0;
  }
  for (a in MIN_B_AGE:(MIN_B_AGE2-1)) {
    p_beadult[a] = inv_logit(bead_lg_mean + bead_lg_re[a - MIN_B_AGE + 1] * sigma_re_bead);
  }
  for (a in MIN_B_AGE2:MAX_AGE) {
    p_beadult[a] = p_br_post;
  }

  for (t in 1:(MAX_T-1)) {
    for (s in 1:N_PDETECTS) {
      p_detect[s, t] = inv_logit(p_detect_lg_mean[s] + p_detect_lg_re[t] * sigma_re_p);
    }
    for (sex in 1:2) {
        s_adult[sex, t]  = inv_logit(surv_ad_lg_mean[sex] + surv_ad_lg_re[sex, t] * sigma_re_ad_s);
    }
  }
```

```
  for (t in 1:MAX_T) {
    p_success[t] = inv_logit(bsucc_lg_mean + bsucc_lg_re[t] * sigma_re_bsucc);
  }

  for (sex in 0:2) {
    p_moveout[sex+1] = sex != 0 ? p_leave[sex] : p_female * p_leave[1] + (1-p_female) * p_leave[2];
    p_movein[sex+1]  = sex != 0 ? p_back[sex]  : p_female * p_back[1]  + (1-p_female) * p_back[2];
    for (t in 1:(MAX_T-1)) {
      s_ad[sex+1, t] = sex != 0 ? s_adult[sex, t] : p_female * s_adult[1, t] + (1-p_female) * s_adult[2, t];
    }
  }

  for (s in 1:N_PDETECTS) {
    for (t in 1:(MAX_T-1)) {
      for (sex in 0:2) {
        p_obs[t, s] = p_detect[s, t];
      }
    }
  }


}


model {

  matrix[N_STATES, N_STATES] tmat;
  matrix[N_STATES_P, N_STATES_P] pmat;

  real temp[N_STATES];

  p_female              ~ beta(1, 1);
  IS_FEMALE             ~ bernoulli(p_female);

  /* Return to colony */
  p_rec                 ~ beta(1, 1);

  /* Becoming an adult (breeding for the first time) */
  p_br                  ~ beta(1, 1);
  p_br_post             ~ beta(1, 1);

  /* Probability of adult to breed (1: failed breeders; 2: non-breeders) */
  p_breed               ~ beta(1, 1);

  /* Survival */
  s_juv                 ~ beta(1, 1);
  s_prebr               ~ beta(1, 1);

  /* Recruitment to colony */
  sigma_re_rec          ~ cauchy(0, 2);
  rec_lg_re             ~ normal(0, 1);
  rec_lg_mean           ~ normal(0, 2);

  /* Becoming adult */
  sigma_re_bead         ~ cauchy(0, 2);
  bead_lg_re            ~ normal(0, 1);
  bead_lg_mean          ~ normal(0, 2);

  /* P(successful breeding) */
  for (n in 1:N_NESTS) {
    NEST_SUCCESS[n]     ~ bernoulli(p_success[NEST_YEAR[n]]);
  }
  sigma_re_bsucc        ~ cauchy(0, 2);
  bsucc_lg_re           ~ normal(0, 1);
  bsucc_lg_mean         ~ normal(0, 2);

  /* P(leaving/returning the study area) */
  p_leave               ~ beta(1, 1);
  p_back                ~ beta(1, 1);

  /* Survival */
  for (sex in 1:2) {
    surv_ad_lg_mean[sex]        ~ normal(0, 2);
    for (t in 1:(MAX_T-1)) {
      surv_ad_lg_re[sex, t]     ~ normal(0, 1); // Time effect varies by sex
    }
  }
  sigma_re_ad_s                 ~ cauchy(0, 2);

  /* Detectability */
  for (s in 1:N_PDETECTS) {
    p_detect_lg_mean[s]         ~ normal(0, 2);
  }
  p_detect_juv                  ~ beta(1, 1);
  p_detect_dead                 ~ beta(1, 1);

  // Same time effect for all classes and sexes (reflects changes in surveys)
  for (t in 1:(MAX_T-1)) {
    p_detect_lg_re[t]           ~ normal(0, 1);
  }
  sigma_re_p                    ~ cauchy(0, 2);
```

```
  /* Likelihood */
  target += reduce_sum(calc_log_sum_multi, INDS, grainsize, N_STATES, SEX, AGE, MAX_T,
                       FIRST_CAP, LAST_CAP, C_HIST,
                       s_ad, s_prebr, s_juv, p_moveout, p_movein,
                       B_SUCCESS, p_breed,
                       p_recruit, p_beadult, p_success,
                       N_STATES_P, p_obs, p_detect_juv, p_detect_dead, p_female,
                       NO_VISIT, FIRST_STATE);

}
```

APPENDIX B MODEL ESTIMATES

Table B-1: Annual survival rate of adults by year and sex, and of pre-breeders and juveniles. Shown are the mean, 95% credible interval (c.i.), and the MCMC trace of the parameter.

Year	Females			Males		
	Mean	95% c.i.	Trace	Mean	95% c.i.	Trace
1994	0.961	0.924 – 0.987		0.959	0.919 – 0.986	
1995	0.970	0.944 – 0.989		0.963	0.933 – 0.986	
1996	0.951	0.917 – 0.977		0.936	0.901 – 0.966	
1997	0.950	0.916 – 0.975		0.950	0.916 – 0.978	
1998	0.924	0.884 – 0.959		0.936	0.900 – 0.965	
1999	0.923	0.881 – 0.959		0.917	0.879 – 0.949	
2000	0.941	0.901 – 0.972		0.941	0.908 – 0.968	
2001	0.935	0.898 – 0.965		0.951	0.924 – 0.975	
2002	0.951	0.925 – 0.973		0.949	0.921 – 0.973	
2003	0.975	0.954 – 0.990		0.965	0.942 – 0.983	
2004	0.941	0.906 – 0.971		0.936	0.907 – 0.960	
2005	0.898	0.806 – 0.969		0.941	0.889 – 0.980	
2006	0.878	0.789 – 0.963		0.933	0.883 – 0.978	
2007	0.883	0.822 – 0.936		0.897	0.853 – 0.935	
2008	0.845	0.776 – 0.911		0.920	0.879 – 0.954	
2009	0.894	0.832 – 0.947		0.914	0.874 – 0.949	
2010	0.906	0.840 – 0.960		0.926	0.889 – 0.958	
2011	0.841	0.770 – 0.906		0.937	0.901 – 0.969	
2012	0.829	0.760 – 0.891		0.911	0.872 – 0.943	
2013	0.821	0.752 – 0.883		0.936	0.902 – 0.963	
2014	0.929	0.876 – 0.970		0.950	0.918 – 0.977	
2015	0.848	0.781 – 0.909		0.914	0.873 – 0.949	
2016	0.871	0.803 – 0.930		0.913	0.871 – 0.949	
2017	0.937	0.884 – 0.977		0.924	0.879 – 0.959	
2018	0.901	0.832 – 0.956		0.916	0.871 – 0.952	
2019	0.908	0.839 – 0.963		0.938	0.894 – 0.972	
2020	0.929	0.861 – 0.976		0.971	0.943 – 0.991	

Age class	Mean	95% c.i.	Trace
Pre-breeders	0.922	0.913 – 0.931	
Juveniles	0.879	0.869 – 0.888	

Table B-2: Probabilities of successful breeding by year. Shown are the mean, 95% credible interval (c.i.), and the MCMC trace of the parameter.

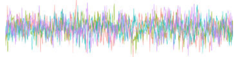
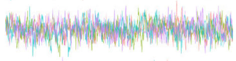
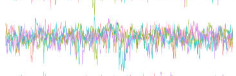
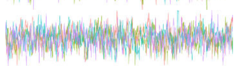
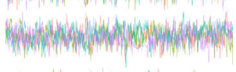
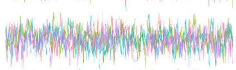
Parameter	Year	Mean	95% c.i.	Trace
P(successful breeding)	1994	0.74	0.67 – 0.81	
	1995	0.74	0.67 – 0.79	
	1996	0.75	0.68 – 0.81	
	1997	0.77	0.71 – 0.83	
	1998	0.73	0.66 – 0.79	
	1999	0.64	0.56 – 0.71	
	2000	0.75	0.67 – 0.81	
	2001	0.75	0.69 – 0.81	
	2002	0.67	0.60 – 0.74	
	2003	0.72	0.66 – 0.77	
	2004	0.71	0.65 – 0.77	
	2005	0.69	0.53 – 0.83	
	2006	0.67	0.48 – 0.81	
	2007	0.60	0.52 – 0.67	
	2008	0.67	0.60 – 0.73	
	2009	0.56	0.47 – 0.65	
	2010	0.67	0.58 – 0.74	
	2011	0.57	0.48 – 0.66	
	2012	0.58	0.49 – 0.67	
	2013	0.61	0.51 – 0.69	
	2014	0.70	0.62 – 0.77	
	2015	0.57	0.47 – 0.66	
	2016	0.66	0.57 – 0.74	
	2017	0.75	0.65 – 0.83	
	2018	0.65	0.57 – 0.73	
	2019	0.61	0.53 – 0.69	
	2020	0.62	0.52 – 0.71	
	2021	0.67	0.48 – 0.81	

Table B-3: Probabilities of returning to the colony and to breed for the first time, as function of age. Shown are the mean, 95% credible interval (c.i.), and the MCMC trace of the parameter.

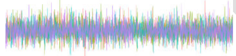
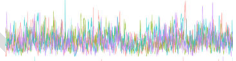
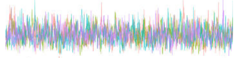
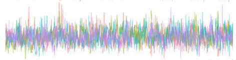
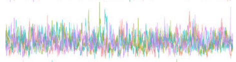
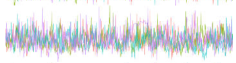
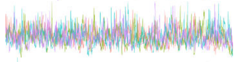
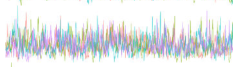
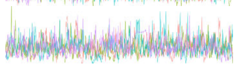
Parameter	Age	Mean	95% c.i.	Trace
P(return to colony)	3	0.03	0.02 – 0.04	
	4	0.11	0.09 – 0.14	
	5	0.10	0.07 – 0.14	
	6	0.29	0.24 – 0.34	
	7	0.33	0.25 – 0.42	
	8	0.69	0.56 – 0.83	
P(breed for first time)	7	0.02	0.01 – 0.04	
	8	0.06	0.04 – 0.09	
	9	0.07	0.05 – 0.10	
	10	0.06	0.04 – 0.09	
	11	0.10	0.07 – 0.14	
	12	0.13	0.09 – 0.18	
	13	0.12	0.08 – 0.17	
	14	0.13	0.09 – 0.18	
	15	0.07	0.04 – 0.12	
	16	0.13	0.08 – 0.19	
	17	0.10	0.05 – 0.16	
	18	0.09	0.04 – 0.15	
	19	0.12	0.06 – 0.20	
	20	0.05	0.02 – 0.10	

Table B-4: Probabilities of adults breeding, that an individual is female, that a bird inside the study area move outside it, and probability that a bird outside the study area returns inside. Shown are the mean, 95% credible interval (c.i.), and the MCMC trace of the parameter.

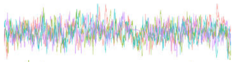
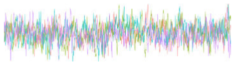
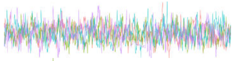
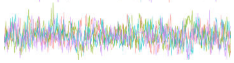
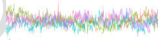
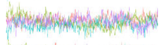
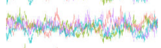
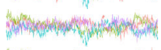
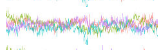
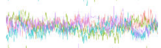
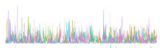
Parameter	Category	Mean	95% c.i.	Trace
P(breeding)	Previously unsuccessful breeders	0.70	0.69 – 0.72	
	Other non-breeders	0.64	0.63 – 0.65	
P(female)		0.51	0.49 – 0.53	
P(leave the study area)	Female	0.09	0.08 – 0.10	
	Male	0.04	0.04 – 0.05	
P(return to the study area)	Female	0.18	0.15 – 0.20	
	Male	0.25	0.22 – 0.29	

Table B-5: Detection probabilities: annual averages, year effect, and interannual variability, as well as the time-invariant detection probabilities of juveniles and dead birds. Shown are the mean, 95% credible interval (c.i.), and the MCMC trace of the parameter.

Parameter	Category	Mean	95% c.i.	Trace
P(detection) - overall	Breeding adult (inside SA)	0.864	0.816 – 0.900	
	Non-breeding adult (inside SA)	0.052	0.036 – 0.072	
	Other non-breeders (inside SA)	0.997	0.992 – 1.000	
	Pre-breeders (inside SA)	0.661	0.575 – 0.736	
	Adults and pre-breeders outside SA	0.180	0.132 – 0.234	
Year effect (logit scale)	1995	-1.388	-2.214 – -0.679	
	1996	1.014	0.471 – 1.605	
	1997	1.529	0.915 – 2.168	
	1998	0.711	0.189 – 1.294	
	1999	0.596	0.058 – 1.152	
	2000	0.238	-0.282 – 0.766	
	2001	0.475	-0.028 – 1.007	
	2002	1.052	0.494 – 1.657	
	2003	1.656	1.044 – 2.305	
	2004	1.475	0.901 – 2.078	
	2005	1.139	0.612 – 1.692	
	2006	0.017	-1.792 – 1.849	
	2007	-1.887	-2.654 – -1.229	
	2008	-0.491	-0.973 – -0.039	
	2009	-0.492	-0.982 – -0.034	
	2010	-0.394	-0.859 – 0.050	
	2011	-1.019	-1.593 – -0.507	
	2012	-0.464	-0.955 – 0.027	
	2013	0.004	-0.457 – 0.462	
	2014	0.329	-0.156 – 0.816	
	2015	-0.383	-0.885 – 0.124	
	2016	-0.395	-0.931 – 0.100	
	2017	-0.079	-0.585 – 0.424	
	2018	0.229	-0.302 – 0.726	
	2019	-0.021	-0.527 – 0.484	
	2020	-1.763	-2.506 – -1.113	
	2021	0.018	-0.536 – 0.565	
Inter-annual variability		0.858	0.638 – 1.169	

Parameter	Mean	95% c.i.	Trace
P(detection) - Juveniles	0.0002	0.0000 – 0.0007	
P(detection) - Dead birds	0.0008	0.0005 – 0.0012