

Cryptic population decrease due to invasive species predation in a long-lived seabird supports need for eradication

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ABSTRACT

1. Invasive species are one of the greatest drivers of biodiversity loss worldwide, and the eradication of invasive species from islands is a highly efficient management strategy. Because eradication operations require large financial investments, uncertainty over the magnitude of impacts of both invasive species and their removal can impede the willingness of decision makers to invest in eradication. Such uncertainty is prevalent for long-lived species that display an inherent lag between life stages affected by invasive species and those used for population status assessments.
2. Albatrosses are among the longest-living bird species and are threatened on land by invasive species and at sea by industrial fisheries. As in many seabird species, usually only a segment of the population (breeding adults) is used for status assessments, making it difficult to assess their population trends and the potential benefit of conservation action, such as the management of predatory invasive species.
3. We used population monitoring and mark-recapture data to estimate the past population trajectory of the Critically Endangered Tristan Albatross (*Diomedea dabbenena*) by accounting for unobservable birds at sea in an integrated population model. We then projected the future population trajectory for scenarios with or without predation by invasive house mice (*Mus musculus*) on their main site, Gough Island.
4. The adult breeding population remained stable between 2004 and 2021, but breeding success was low (31%) and our model indicated that the total population (including unobservable immature birds) decreased from a median estimate of 9795 to 7752 birds. Eradicating invasive mice leading to a two-fold increase in breeding success would result in a 1.8–7.6 times higher albatross population by 2050 (median estimate 10 352 individuals) than without this intervention.
5. Low reproductive output for long-lived species may lead to a cryptic population decrease, which can be obscured from readily available counts of breeding pairs by changes in the population structure. Mouse eradication is necessary to halt the ongoing population decrease of the Tristan Albatross, even if this decrease is not yet apparent in the breeding population size.

Key Words: albatross, mark-recapture, integrated population model, population viability analysis, demography, life-history, conservation management, invasive species eradication

Introduction

Invasive non-native species are one of the greatest drivers of biodiversity loss worldwide, especially for species endemic to oceanic islands (Bellard, Cassey & Blackburn 2016; Maxwell *et al.* 2016; Spatz *et al.* 2017). Accordingly, the eradication of invasive species from islands is a highly efficient management tool that has benefitted hundreds of threatened species on many islands around the world (Howald *et al.* 2007; Jones *et al.* 2016; de Wit *et al.* 2020). However, eradicating invasive species typically requires large financial investments (Martins *et al.* 2006; Holmes *et al.* 2015; Wenger *et al.* 2017). Uncertainty over the severity of impacts resulting from invasive species, as well as the potential benefits of invasive species removal, can therefore impede willingness to invest in eradication as a management action (Bomford & O'Brien 1995; Helmstedt *et al.* 2016)

Predation by invasive non-native species is also one of the greatest threats to long-lived seabird species, which are a highly threatened group of birds (Dias *et al.* 2019). However, estimating the effects of invasive species on seabird populations is complicated by the complex life history strategy of seabirds (Bakker *et al.* 2018). For example, delayed maturity means that a substantial proportion of the population, composed of juveniles and immature birds, is largely unobservable because these birds spend many years at sea prior to first breeding (Croxall & Rothery 1991; Brooke 2004). This delayed maturity creates an inherent lag between the demographic parameters predominantly affected by invasive species (breeding success), and the observable components of a population used to assess conservation status (Klomp & Furness 1992; Votier *et al.* 2008). Procellariiformes (albatrosses and petrels) have the longest time periods between fledging and maturity amongst seabirds (5-15 years; Ricklefs 1990; Brooke 2004), and many albatrosses do not attempt to breed in the year after raising a chick, further increasing the number of individuals that are not observable at the breeding colony (Pardo, Barbraud & Weimerskirch 2013; Carneiro *et al.* 2020). Consequently, annual counts of breeding pairs, or individuals at the colony, may not immediately reflect the impact that invasive non-native species can have on seabird population dynamics, and an observable population response following either the introduction or the successful eradication of invasive species may take decades (Jones 2010; Jones *et al.* 2021).

Quantifying the impact of invasive alien species on seabirds is further complicated by changing interactions between native and invasive species due to environmental changes over time. Both the consequences of a warming climate (McClelland *et al.* 2018) and the depletion

of food sources at lower trophic levels (Russell *et al.* 2020) can progressively alter the foraging tactics of invasive species. Over time, the impact of invasive species on long-lived native vertebrates may therefore increase (Davies *et al.* 2015; Jones *et al.* 2019), such that the potential benefit of an eradication would be greater than that estimated using current levels of predation. Although the benefit of eradicating invasive species has been demonstrated for many species on hundreds of islands, these studies have so far lacked long-term monitoring (Brooke *et al.*, 2018; Jones *et al.*, 2016). Realistic predictions of likely population responses would facilitate the selection of suitable long-term monitoring programmes that are both logistically feasible and likely to capture population responses (Wauchope *et al.* 2019). Consequently, there is a pressing need to quantify future population responses after invasive species eradication to guide investment in both management actions and monitoring programmes (Dawson *et al.* 2015; Helmstedt *et al.* 2016; Holmes *et al.* 2019).

Here we demonstrate, with the example of a long-lived albatross, how a cryptic population decrease can be caused by an invasive species, and then quantify the likely outcomes of an eradication on this albatross population. By accounting for biennial breeding and unobservable immature birds at sea in an integrated population model, we estimate the global population trend of the Critically Endangered Tristan Albatross (*Diomedea dabbenena*) and contrast this estimate with the observable size of the breeding population between 2004 and 2021. We then use this model to predict population trajectories under three plausible scenarios, namely a successful eradication of the invasive house mouse (*Mus musculus*), or the persistence of mice at current or gradually worsening levels of impact. The results of our study provide quantitative estimates to inform monitoring and management decisions and highlight the value of population models to reveal demographic processes in long-lived species that are difficult to observe directly.

Material and methods

Study species and existing management options

The Tristan Albatross breeds almost exclusively on Gough Island (40° 21' S, 9° 53' W), a natural World Heritage site located in the central South Atlantic Ocean as part of the UK Overseas Territory of Tristan da Cunha, with only ~2 breeding pairs elsewhere in the world (on Inaccessible Island; Ryan, Dilley & Ronconi 2019). The demography of the species was last analysed in 2007, and at that time low annual survival (adult 0.91, juvenile 0.76) due to bycatch in longline fisheries across the South Atlantic Ocean threatened the persistence of the

species (Cuthbert *et al.* 2004; Wanless *et al.* 2009). Tristan Albatrosses are also affected by low breeding success due to chick predation by invasive house mice (Cuthbert & Hilton 2004; Wanless *et al.* 2007; Wanless *et al.* 2009; Davies *et al.* 2015). Mice have been present on Gough since the 19th century and have affected breeding success of seabirds since at least 2000 when the low breeding success was first noticed (Cuthbert & Hilton 2004; Wanless *et al.* 2007). Mice have recently been observed attacking adult albatrosses and could cause increased rates of adult mortality in the future, either by direct predation or by facilitating predation by other birds (Jones *et al.* 2019; Risi *et al.* 2021).

Due to the threats at sea (fisheries bycatch) and on land (invasive mice), management to improve the conservation status of the Tristan Albatross has separately focussed on these two major threats. Advances in bycatch mitigation in key foraging areas (Dias *et al.* 2017; Jiménez *et al.* 2020; Da Rocha *et al.* 2021) may have increased the at-sea survival probability of Tristan Albatrosses, and further expansion of mitigation measures and fisheries management are one management option that is beyond the scope of our analysis here. The threat of invasive mice can realistically only be reduced by eradicating mice from Gough Island, because long-term control or measures to protect nests from mice are not practically feasible at a scale that would be relevant to the population. Mouse eradication is therefore the sole management option against the threat of invasive mice, but due to the limited information on current demographic parameters, the potential population trajectory after a mouse eradication has been difficult to quantify. A mouse eradication attempt was carried out in the austral winter of 2021, but the operation was not successful and invasive mice therefore remain on Gough Island.

Monitoring data for population size and breeding success

Tristan Albatrosses breed in open upland heath and bog habitat on Gough Island. While partial population counts occurred in 1999, 2002, and 2003, the breeding population has been counted comprehensively across the island first in 2001 and then twice a year since 2004 (Ryan, Cooper & Glass 2001; Cuthbert, Cooper & Ryan 2014). Tristan Albatrosses lay eggs in January, and we counted the number of breeding pairs in late January or early February in eight study areas that cover the breeding range on Gough Island (Ryan *et al.* 2001; Cuthbert *et al.* 2014). We recorded the number of nests (equivalent to breeding pairs) per study area, which are delineated by ridgelines and valleys, because these areas are exposed to different weather conditions and have different topography, and may therefore be subject to different errors in counts of breeding pairs. The sum of breeding pairs across our study areas reflects

the global breeding population of the species. Breeding success was assessed by counting large chicks in late September in the same eight study areas where breeding pairs were counted. Because albatrosses lay only one egg and can raise only one chick, the ratio of large chicks counted in September to the number of breeding pairs in January reflects the annual breeding success, i.e. the proportion of eggs successfully reared to fledging (Cuthbert *et al.* 2004; Caravaggi *et al.* 2019). All data collections were authorised by the Tristan da Cunha Conservation Department under annual research permits.

Individual mark-recapture data

Albatrosses have been individually marked with uniquely numbered metal rings in some study areas on Gough Island since 1979, but intensive monitoring of breeding pairs and non-breeding loafers (pre-breeders and non-breeding adults) commenced in 2001 (Cuthbert *et al.* 2004; Wanless *et al.* 2009). All adult breeding birds and non-breeding loafers in two of the eight study areas (~200 pairs annually) were examined during each of several colony visits each breeding season and identified based on their unique ring number. Since 1980, most fledglings in these two study areas have been ringed as well. We built mark-recapture encounter histories for each ringed individual, where the encounter history entry $e_{i,t}$ = '1' if individual i was observed, as either a breeder or loafer, at least once in year t , and '0' otherwise. Overall, we had individual encounter histories for 4014 Tristan Albatrosses from 1979 to 2021, of which 947 were ringed as adults of unknown age, and 3067 were ringed as fledglings. All birds were ringed under the South African ringing scheme (until 2018) and the British Trust for Ornithology (since 2019).

Given that large albatrosses in open terrain are highly visible, approachable, and faithful to their established breeding site once they have started breeding, the probability that a breeding individual will be detected and identified is very high if the nest does not fail early. Early failures leading to non-detection are rare because the colony is visited at least weekly until both partners at each nest have been identified. Thus, we assumed that the detection of adults after their initial return to the colony was virtually perfect, such that the 'detection' probability estimated in our survival model (described below) primarily reflected the probability of returning to the island and breeding given that the bird had survived.

Estimating population size and trajectory in an integrated population model

We used an integrated population model adapted from similar models for other seabird species (Szostek, Schaub & Becker 2014; Abadi, Barbraud & Gimenez 2017; Genovart, Oro

& Tenan 2018; Seward *et al.* 2019) to combine the demographic and population size data sets into one analytical framework and simultaneously estimate the demographic parameters and population size of Tristan Albatrosses between 2004 and 2050 (Fig. 1; mathematical description in Supplementary Information). An integrated population model provides a joint analytical framework to model both annual abundance data and demographic parameters simultaneously in a single model, which generally leads to more precise parameter estimates and accounts for the uncertainty in demographic parameters in population projections (Besbeas *et al.* 2002; Schaub & Abadi 2011; Zipkin & Saunders 2018).

Our population model was based on an age-structured female-based matrix model with 31 different age classes to account for the delayed age at which Tristan Albatrosses may breed for the first time (Cuthbert *et al.* 2004; Weimerskirch 2018). Based on our ringing data, we specified that birds could first return to the breeding grounds at the age of two years, and that the probability of returning for the first time would increase logistically with age up to 30 years, which was the maximum observed age for an individual to be first detected after fledging. Once a bird had returned for the first time, the probability of returning in subsequent years was dependent on the previous year's breeding history, because it is extremely rare for Tristan Albatrosses to attempt breeding in a year following a successful breeding attempt (Ryan *et al.* 2001).

As observed in other seabird species, we assumed that the survival probability of birds in their first year at sea was lower than for birds older than one year (Horswill & Robinson 2015; VanderWerf & Young 2016). We allowed probabilities of survival, return and detection on Gough Island, and breeding success to vary from year to year, which is supported by previous findings in other large albatross species (Pardo *et al.* 2017; Weimerskirch 2018; Cleeland *et al.* 2021). To reduce model complexity and ensure parameter identifiability, we assumed an equal sex ratio amongst fledglings, and no difference in annual survival between sexes, which is supported by evidence from albatross populations where sex-specific survival has been examined (Weimerskirch, Lallemand & Martin 2005; Pardo *et al.* 2013; Pardo *et al.* 2017).

Using the mark-recapture encounter histories, we estimated annual survival probability between 1979 and 2022 within the integrated population model using an age-structured Cormack-Jolly-Seber model for two age classes. We chose a multinomial likelihood formulation because an individual formulation was computationally prohibitive (Lebreton *et al.* 1992; Kéry & Schaub 2012; Seward *et al.* 2019). The probability of being observed and recorded on Gough Island was assumed to be different for birds returning to

Gough Island for the first time, because immature loafers generally visit the breeding areas later in the year and are therefore less likely to be detected than established birds that spend more time on breeding grounds. Established birds, after their first return, are detected with near certainty if they return to the study area, and we therefore used the ‘detection’ probability estimated in the survival component of the model as the probability of returning to the island in the population process component of the model. We did not model the dependence of return probability on previous breeding success at the individual level, because historical monitoring data did not contain comprehensive information on breeding outcome for individual breeders.

The survival component of the population model therefore had six parameters describing the mean annual survival for birds in their first year and for older birds, and mean detection probabilities for young birds and birds after their first observed return to the colony in high- and low effort years, respectively. Four random distributions allowed for annual variation in these parameters. Because the estimation of annually varying juvenile survival probability (from fledging to age 1) requires a sufficient sample size, we were not able to estimate a random offset for juvenile survival in every year. Therefore, we assumed that the juvenile survival probability in those years where fewer than 70 fledglings were ringed ($n = 9$ out of 43 years) was equal to the overall mean across all years. Because the effort to record ringed birds and to ring fledglings varied over time and increased markedly after 2004, we divided years into those with high survey effort (defined as 2001 and 2004–2022) and those with low survey effort (prior to 2001, 2002 and 2003), and used separate detection intercepts for high and low survey effort years. Our assumption that detection probability reflected the probability to return to the island was limited to those years with high survey effort.

To estimate the probability that pre-breeding birds return to the breeding grounds for the first time, we used the ages at which birds ringed as fledglings were first recorded on Gough Island as immatures or as breeders within the survival component of the integrated population model. We used these data to inform the estimated probability of returning at a given age and used this age-specific probability in our population process component of the model to draw the proportion of immature birds of a given age group that first returned to breeding grounds in each year. The minimum age of first breeding recorded in our study was 4 years, but data on the exact age at which birds marked as chicks started breeding were not available for most birds. We therefore made the explicit assumption that for birds at ages of 4 years and older, the probability to return to breeding grounds as estimated from our mark-recapture data was equal to the probability to recruit into the breeding population (Fig. 1). We

consider this assumption realistic given that immature pre-breeders usually visit the colony later in the breeding season, but routine recording of ringed non-breeders at that time of the season increased only from 2009 onwards, hence the majority of young birds were unlikely to have been recorded on breeding grounds prior to their first breeding attempt in our time series.

The annual breeding success was estimated assuming that the annual number of large chicks counted in our study areas in September followed a Poisson distribution with parameters that were the product of the annual number of observed pairs counted in the same study areas in January and the breeding success. Because chicks fledge in December, the September count may provide a slightly optimistic estimate of breeding success. However, our data suggest that very few chicks die in the 3 months between the count and fledging (Cuthbert *et al.* 2014). Moreover, any mortality that occurred between the count of chicks and fledging would be accounted for by the estimate of annual juvenile survival in our model and would therefore not introduce any bias into our modelled population process.

To relate our estimates of breeding success and survival to the annual census data of breeding pairs on Gough Island, we used a hierarchical state-space model (de Valpine 2003; Clark & Bjørnstad 2004; Kéry & Schaub 2012) for the annual census data. Because data included gaps for certain study areas due to fog and poor visibility, we modelled the population size in each study area independently, which allowed us to account for missing data from certain study areas and varying observation error due to the different topography of the study areas. To relate the overall population size to the number of breeding pairs observed in each study area, we multiplied the expected breeding population size calculated in our demographic model by the long-term average proportion of observed breeding pairs in each study area and related the observed count of breeding pairs in that study area to the expected breeding population size. The full population process on which the model was based can be found in the Supplementary Information.

We used a Bayesian framework for inference and parameter estimation because it provided sufficient flexibility and allowed for the incorporation of existing information to inform prior distributions for demographic parameters (Wade 2000; Brooks, King & Morgan 2004; Schaub *et al.* 2007). Specifically, estimating the number of unobservable immature birds in certain age classes in the first model year (2004) required the selection of informative priors. We used breeding success and ancillary count data from 1999 to 2003 to inform prior distributions for the number of immature birds that existed in 2004 in age classes from 1 to 5 years of age, because estimates based on a stable age structure inferred from a Leslie matrix

did not account for the annual variation in number of breeding pairs and juveniles. Thus, our population model deliberately did not start in the year with the first census data (2001), but used the ancillary information to inform the population process from 2004 onwards. For demographic parameters, we used priors based on previous studies of large albatrosses elsewhere (Elliott & Walker 2005; VanderWerf & Young 2016; Pardo *et al.* 2017; Weimerskirch 2018), and specified priors for both adult and juvenile survival with beta distributions (adult survival with $\alpha = 91$ and $\beta = 9$, resulting in mean = 0.910 and variance = 0.0008; and juvenile survival with $\alpha = 75.7$ and $\beta = 24.3$, resulting in mean = 0.757 and variance = 0.002). We used diffuse uniform priors (0–1) for return probabilities for adults and immatures, because these probabilities reflect the probability to return and breed, which can vary annually depending on breeding success in the previous year. The prior for annual breeding success was specified with a beta distribution with $\alpha = 32$ and $\beta = 68$, resulting in mean = 0.319 and variance = 0.002, as albatrosses lay a single egg and the Tristan Albatross breeding success is chronically low due to mouse predation (Wanless *et al.* 2009; Caravaggi *et al.* 2019). We used an exponential prior with $\lambda = 0.1$ for the standard deviation of the observation error in the counts of breeding pairs, and with $\lambda = 1$ for the standard deviation of the random year effect in juvenile re-sighting and survival probabilities.

We fitted the integrated population model in JAGS (Plummer 2012) called from R 4.1.1 (R Core Team 2021) via the package ‘runjags’ (Denwood 2016). We ran three Markov chains with an adaptive phase of 20 000 iterations. We discarded a burn-in of 25 000 iterations and thinned the remaining samples by 10, yielding 200 000 samples per chain from all iterations. One model run took 75 hours to complete on a 3.4 GHz processor with 64GB random-access memory. We tested for convergence using the Gelman-Rubin diagnostic (Brooks & Gelman 1998) and confirmed that the chains were well-mixed, with $\hat{R} < 1.1$ and effective sample sizes > 500 for all parameters. We present posterior median estimates of parameters with 95% credible intervals.

To contrast the results of our integrated population model with a basic interpretation of observed raw data, we also present a linear regression of the observed number of breeding pairs between 2004 and 2021, thereby estimating a naïve apparent trend in the population based on the trend in number of breeders. In addition, the results of our integrated population model prompted three further questions to understand the demographic processes leading to the discrepancy between observed and estimated population trajectory. We examined whether annual breeding success estimated from our raw data changed over time in a generalized linear model with a binomial error structure. We further examined whether the proportion of

individually marked breeding birds of known age that were older than 30 years (when reproductive performance becomes more variable; Froy *et al.* 2013) changed over time in a generalized linear model with a binomial error structure and a complimentary log-log link function. We weighted the annual proportions by annual observation effort, and included the proportion of ringed birds of breeding age that had been ringed ≥ 30 years previously as an offset to correct for the fact that more birds of older age were available in our data set in later years. Lastly, we examined whether the age at which birds ringed as chicks were first observed returning to the breeding colony changed over time in a generalized linear model with a Poisson error structure and weighted for annual observation effort. Correlations between demographic parameters and the annual population growth rate were calculated using a Pearson correlation coefficient and are presented in the Supplementary Information.

Population projections under different scenarios

We were interested in the future population trajectory of Tristan Albatrosses on Gough Island under three realistic scenarios reflecting whether mice could be successfully eradicated or not: (1) persistence of mouse predation at levels observed from 2004 – 2021 such that there would be no change in mean annual breeding success and survival; (2) successful mouse eradication leading to an immediate increase of annual breeding success of Tristan Albatrosses (to the value of other great albatrosses on predator-free islands, 0.63; Caravaggi *et al.* 2019) with no changes in survival; or (3) persistence of mouse predation on chicks at levels observed from 2004 – 2021, and gradual increase of mouse predation of adult albatrosses such that adult survival decreases by 10% over the next 10 years (McClelland *et al.* 2018; Jones *et al.* 2019; Russell *et al.* 2020).

We used the integrated population model to project the population size 30 years into the future while accounting for the uncertainty in demographic parameters (Kéry & Schaub 2012; Oppel *et al.* 2014; Zipkin & Saunders 2018). We included survival probabilities for the two age classes, mean breeding success, and incorporated the three scenarios of plausible changes in breeding success or survival. For each of the three scenarios, we calculated the future albatross population growth rate as the geometric mean of the population growth rate from 2021–2050. We report the median (and 95% credible interval) of this future growth rate as well as the probability of the growth rate being positive as the proportion of simulations where the growth rate was >1 . We also quantified the theoretical benefit of a mouse eradication as the difference in albatross population size in 2050 between the three scenarios. We used the posterior distribution of future population sizes to present the probability of the

future population being larger with than without mouse eradication, and the probability that the population in 2050 would be greater than in 2004 at the beginning of our time series.

Results

The number of observed Tristan Albatross breeding pairs on Gough Island fluctuated between 1106 and 1921 between 2004 – 2021, and there was no evidence for a decrease in the breeding population over those 16 years (linear regression $\beta = -6.02 \pm 12.20$ standard error, $p = 0.628$; Fig. 2). However, when considering the total population size, including the unobservable immature and non-breeding birds, we found a statistically detectable decrease in the global population from an estimated median of 9795 individuals (95% credible interval 9504 – 10,129) in 2004 to 7752 individuals (7276 – 8240) in 2021, a decrease of 1% per year (Table 1, Fig. 2). Annual breeding success was 0.31 fledglings per pair and varied between 0.15 (in 2008) and 0.54 (in 2013), with no significant trend over time ($\beta = 0.002 \pm 0.005$, $p = 0.720$, Fig. S1). Mean annual juvenile (0.821) and adult survival probabilities (0.948) were most strongly correlated with annual population growth rates (Fig. S3). Because survival was sufficiently high to maintain a stable population (Table 1), the long-term population decrease was likely explained by the overall low breeding success, which was the only demographic parameter that differed between two of our future projections (Fig. 2).

Projecting the Tristan Albatross population into the future revealed different outcomes for our three scenarios (Fig. 2), with a global population gradually decreasing by 1% per year if mouse predation would persist at current levels (probability of positive population growth rate 8%, Fig. 3). By contrast, the albatross population would likely recover to a median of 10 352 individuals (5358–17 264) in 2050 under a successful mouse eradication and a concomitant increase in annual breeding success to a value typical for large albatrosses on predator-free islands (probability of positive population growth rate 83%; Fig. 3). Our most pessimistic scenario, that mouse predation of chicks would persist at current levels and predation of adults would gradually increase, led to an increasingly rapid population decrease, with an average rate of ~6% per year until 2050 (probability of positive population growth rate 0%; Table 1, Fig. 3) and a probability of 18% that the total population would fall below 500 individuals.

We estimated the benefit of a successful mouse eradication on Gough Island to be that the Tristan Albatross population in 2050 would be 1.8 (1.7–1.9) times higher following a successful eradication than if no eradication was conducted, or 7.6 (7.2–8.2) times higher

than if no eradication was conducted and mice would increasingly prey upon adult albatrosses (Fig. 2). The probability that the Tristan Albatross population in 2050 would be greater after a successful mouse eradication than without a mouse eradication was 94% (when assuming no future change in mouse predation) or 100% (if mouse predation would increase, Fig. S2). The probability that the total population in 2050 was greater than the population in 2004 was 57% after a successful eradication, 1.3% without an eradication and constant impact of mice, and 0% without an eradication and worsening impact of mice (Fig. S2).

The observable breeding population of Tristan Albatrosses may have remained stable between 2004 and 2021 despite a decreasing global population size due to changes in the structure of the breeding population. The proportion of breeders that were older than 30 years increased from 2.6% in 2004 to 6.7% in 2021, but that increase was confounded by the rapidly increasing proportion of birds that had been ringed >30 years ago, and we were therefore unable to attribute that increasing proportion to a biological process ($\beta = 0.057 \pm 0.03$; $p = 0.85$). Similarly, the average age at which birds ringed as chicks were first recorded back on breeding grounds on Gough Island decreased from ~14 years in 2004 to ~7 years in 2021 ($\beta = -0.042 \pm 0.004$; $p < 0.001$), but this effect could have occurred due to an increase in recording effort.

Table 1. Demographic parameter estimates of the Tristan Albatross (*Diomedea dabbenena*) population breeding on Gough Island estimated with an integrated population model based on count and breeding success data from 2004 – 2021, and mark-recapture data from 1979 – 2022. Three scenarios for projecting the future population trajectory were considered: (1) persistence of mouse predation at current levels; (2) successful mouse eradication in 2021 leading to immediate increase in breeding success; and (3) persistence of mouse predation at current levels with increased predation of adult birds.

Demographic parameter	Median	95% credible limit
Mean annual adult survival probability	0.948	0.936 – 0.961
Mean annual juvenile survival probability	0.821	0.768 – 0.870
Mean annual productivity	0.312	0.305 – 0.320
Population growth rate λ (2004-2021)	0.986	0.983 – 0.990
Predicted future growth rate λ (2021-2050) without change	0.989	0.973 – 1.005
Predicted future growth rate λ (2021-2050) with successful eradication	1.010	0.992 – 1.029
Predicted future growth rate λ (2021-2050) with increasing mouse impacts	0.939	0.924 – 0.954

Discussion

We estimate that the global Tristan Albatross population has decreased by ~1% per year from 2004 to 2021 despite the apparent stability of the observed number of breeding pairs on its main breeding island in the South Atlantic Ocean. Low breeding success led to a decreasing number of immature albatrosses available to recruit into the breeding population, but the decreasing global population size may have been obscured by a changing composition of the breeding population, thus leading to a constant observable number of breeding pairs (Klomp & Furness 1992; Votier *et al.* 2008). A successful mouse eradication that would lead to an immediate increase in breeding success could allow the population to recover slowly, resulting in a Tristan Albatross population 1.8–7.6 times greater by 2050 than without a mouse eradication on Gough Island.

The Tristan Albatross was classified as ‘Critically Endangered’ following a previous demographic analysis that concluded that increasing the breeding success alone would not be sufficient to reverse population decreases and that the species might go extinct within 30 years (Wanless *et al.* 2009). This result was partly due to low mean annual adult survival probability (0.91). However, recent efforts to reduce bycatch mortality in several South Atlantic fisheries (Jiménez *et al.* 2020; Da Rocha *et al.* 2021) may have contributed to the higher mean adult survival that we estimated in this study for the same population 15 years later (0.948, Table 1). Our results suggest that the Tristan Albatross now has a similar annual adult survival probability to other large albatrosses with stable populations elsewhere (0.957 for *D. amsterdamensis*, Weimerskirch, Brothers & Jouventin 1997; 0.957 for *D. antipodensis antipodensis* and 0.961 for *D. a. gibsoni*, Elliott & Walker 2005; >0.95 for *D. exulans*, Weimerskirch *et al.* 2018). We show that combining this adult survival with an increased breeding success associated with a successful mouse eradication could result in a slow recovery of the Tristan Albatross population, as has been observed for Wandering Albatross (*D. exulans*) populations in the Indian Ocean, which showed signs of recovery after strong decreases in the 1970s (Weimerskirch *et al.* 2018). However, the gains in the survival probability of adults resulting from bycatch reduction could be reversed if mice remained on Gough Island and increasingly preyed upon adults (Jones *et al.* 2019).

The population decreases of other albatrosses in the Southern Ocean are assumed to be caused by the impacts of fisheries and climate change (Pardo *et al.* 2017; Cleeland *et al.* 2021; Rackete *et al.* 2021), and are similar in scale to the population decrease we found for Tristan Albatrosses. Our results suggest, however, that it is mostly the effect of invasive mice

on breeding success that is causing the decrease of Tristan Albatrosses, and that the population could likely recover once this threat has been removed. Population recovery in species with low reproductive rates can take decades to be detectable, and any assessment of the benefits of conservation interventions should take this into account (Brooke *et al.* 2018). Future monitoring of Tristan Albatrosses would likely need to include a population census every few years for at least 3–5 decades to reveal any change in the observable breeding population (Wauchope *et al.* 2019). Deciding on an efficient future monitoring programme is complicated by the considerable uncertainty in the future projections of the Tristan Albatross population after a successful mouse eradication on Gough Island. As expected for species with long life-history strategies, our study indicates that any increase in the population would likely be slow, such that by 2050 there was only a 57% probability under our most optimistic scenario (successful mouse eradication) that the total population size would be greater than it was in 2004 when our study began. Alternatively, it is possible that despite increasing breeding success the population could continue to decrease, albeit at a slower rate. This uncertainty in the future population trajectory is due to the large annual variation and uncertainty in juvenile survival in the first year at sea.

Young albatrosses are more vulnerable to bycatch in fisheries than are adults (Gianuca *et al.* 2017; Frankish *et al.* 2021), and we estimated that Tristan Albatrosses have similar rates of juvenile survival (0.821, Table 1) as other albatrosses (0.757 in *Phoebastria immutabilis*, VanderWerf & Young 2016; 0.680-0.949 for *D. exulans* and 0.764 for *Thalassarche chrysostoma*, Pardo *et al.* 2017; Weimerskirch 2018; 0.75 for *Thalassarche melanophris*, Ventura *et al.* 2021). Tristan Albatrosses forage in areas with high long-line fishing intensity (Dias *et al.* 2017; Carneiro *et al.* 2020), and those fisheries are less regulated than those around subantarctic islands, including South Georgia (Handley *et al.* 2020). Several albatross populations on predator-free islands in South Georgia are declining (Pardo *et al.* 2017; Rackete *et al.* 2021), whereas Black-browed Albatrosses (*T. melanophris*) breeding in the Falkland Islands/Malvinas are increasing (Ventura *et al.* 2021). Bycatch in poorly regulated fisheries in the high seas of the Atlantic Ocean that affect juvenile albatrosses of several species is likely the main reason for the decreases of some populations. Hence, further improvements in the adoption and implementation of effective bycatch mitigation measures are required across the entire range of roaming juvenile albatrosses to improve their survival at sea (Clay *et al.* 2019; Jiménez *et al.* 2020; Frankish *et al.* 2021).

In contrast to other decreasing albatross populations, the Tristan Albatross appears to maintain a stable population of breeding pairs despite low breeding success and decreasing

overall population size. This pattern could be caused by gradually decreasing breeding success, which would allow an increasing proportion of adult birds to breed in subsequent years (after failure). Because we found no indication of a trend in breeding success (Fig. S1), we consider it more likely that the breeding population has been growing collectively older due to a lower number of recruiting immature birds (Porter & Coulson 1987). In addition, immature birds may return at a younger age to breeding grounds and eventually recruit at a younger age, thereby obscuring the overall decrease in population size. We caution, however, that the meticulous recording of immature birds only began in 2009, and the apparent trend of birds returning at a younger age may have been caused by increasing efforts to record loafing birds later in the breeding season. Similarly, our ringing efforts only began in 1979, and the increasing proportion of birds older than 30 years was sufficient to explain most of the variation in the age of our breeding population, hence we cannot conclusively state that the age structure of the breeding population has changed over time. Nonetheless, the gradual senescence of the breeding population and the earlier return of immature birds appear to be the most plausible processes that would lead to an apparently stable breeding population despite a decreasing overall population size (Votier *et al.* 2008; Genovart *et al.* 2018; Sergio *et al.* 2021).

In summary, we conclude that the total Tristan Albatross population has been decreasing over the last two decades, despite a stable number of observed breeding pairs. A successful mouse eradication is very likely to allow the Tristan Albatross population to recover. However, due to the long life span and delayed maturity of albatrosses, any population recovery will likely take many decades (Jones 2010), and may be very difficult to infer in the short term from counting adult breeding pairs. Monitoring breeding success, and recording the identity and age of breeding birds would be most useful for estimating the benefits of an eradication operation because this information is highly likely to allow more timely inference on the population status than monitoring the number of breeding pairs alone.

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Conflict of Interest

The authors declare that they have no conflict of interest.

Author's Contributions

Steffen Oppel, Richard Cuthbert, Sarah Converse, Ross Wanless, Alexander Bond, John Cooper and Peter Ryan conceived the ideas; Steffen Oppel, Sarah Converse, Bethany Clark and Catharine Horswill designed methodology and executed analysis; John Cooper, Peter Ryan, Richard Cuthbert, Ross Wanless, Michelle Risi, Christopher Jones, Alexis Osborne, Kim Stevens, Vonica Perold, Alexander Bond and Steffen Oppel collected and managed the data; Steffen Oppel and Bethany Clark led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data Availability Statement

Data and code to replicate the analysis are available via the Zenodo digital repository <https://doi.org/10.5281/zenodo.6541370> (Oppel & Clark 2022).

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FIGURE LEGENDS

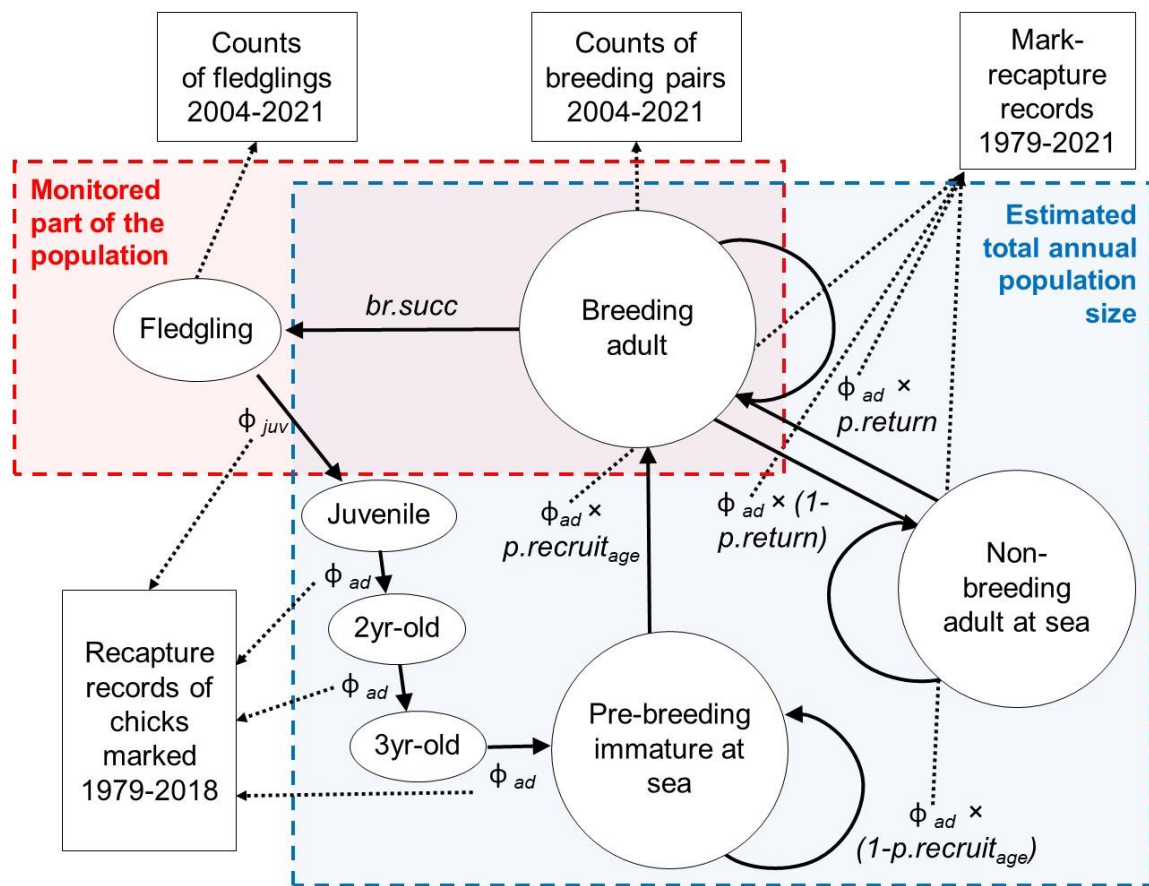


Figure 1. Schematic depiction of the structure of the integrated population model used to assess Tristan Albatross population size and changes over time; the available data (white boxes) informed (dotted arrows) population components (circles) and demographic parameters (solid arrows where Φ = survival, p = recruit or return probability, $br.succ$ = breeding success), and total population was estimated as the sum of all population components including those that could not be observed (blue box). Note that some non-breeding individuals aged 2 years or older can be encountered on Gough Island, but they do not contribute to the counts of breeding adult birds.

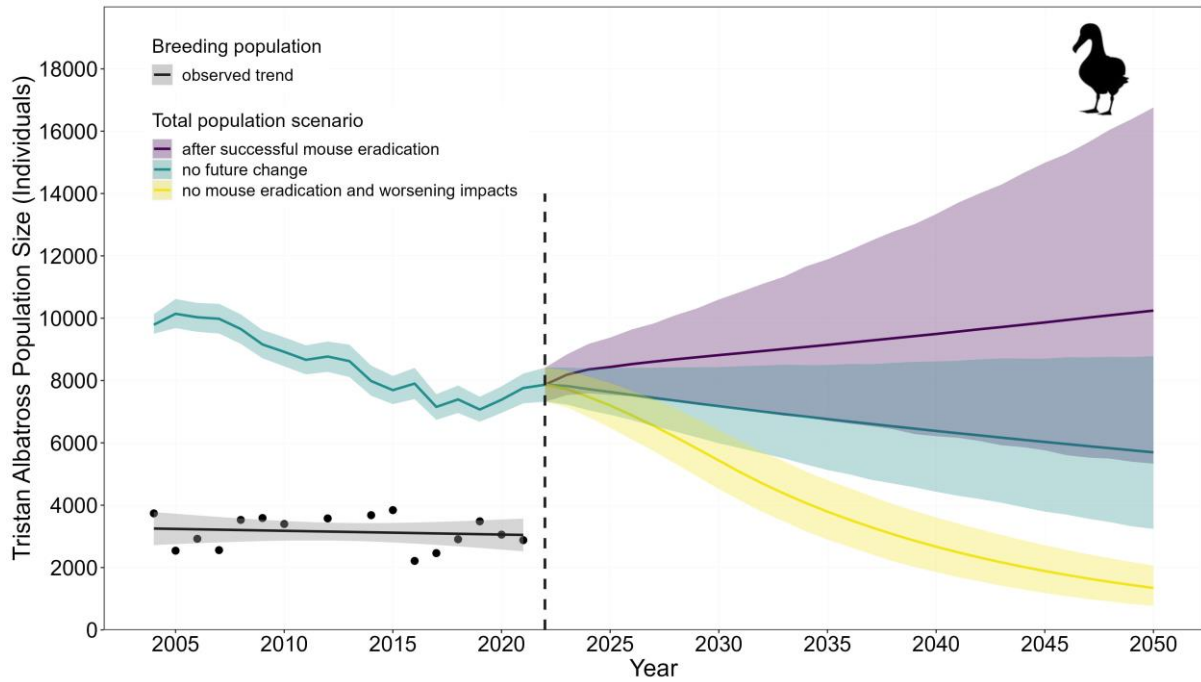


Figure 2. Observed breeding population size of Tristan Albatross on Gough Island between 2004 and 2050 (black points and trend line) and estimated total population size between 2004 and 2050 (coloured). The green line presents the total estimated population size including unobservable immature and non-breeding birds at sea from 2004 to 2021. We considered three scenarios for future population trajectory: successful mouse eradication (purple), persistence of mouse predation at current levels (green) and increasing predation of adult birds with mouse predation of chicks persisting at current levels (yellow). Median values shown as dark line and 95% credible interval with shading. Vertical dashed line indicates separation between retrospective analysis and future projections.

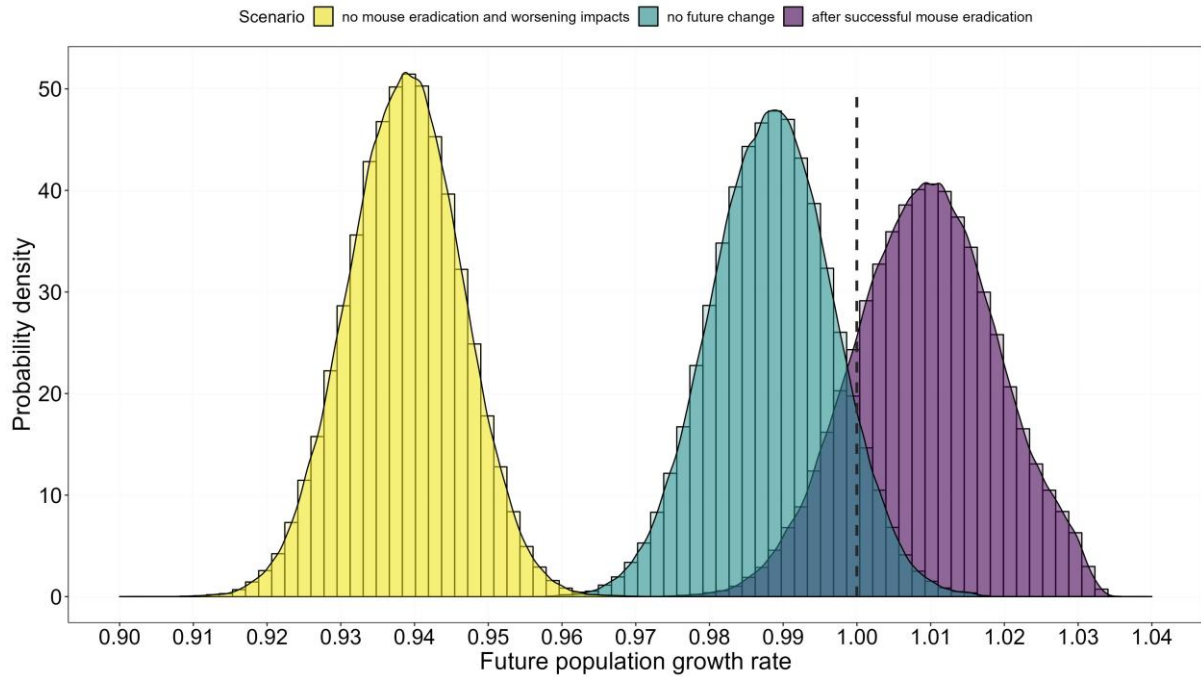


Figure 3. Probability distribution of projected future population growth rate (2021 – 2050) of Tristan Albatrosses estimated with an integrated population model under three plausible management scenarios for future population trajectory: successful mouse eradication (purple), persistence of mouse predation at current levels (green) and increasing predation of adult birds with mouse predation of chicks persisting at current levels (yellow). The vertical dashed line indicates a stable population with a population growth rate of 1.