From both sides: Dire demographic consequences of carnivorous mice and longlining for the Critically Endangered Tristan albatrosses on Gough Island

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ABSTRACT

The IUCN recently uplisted the Tristan albatross (*Diomedea dabbenena*) to Critically Endangered. Here we present new data indicating negative population trends on Gough Island arising from low adult survival (~91%, ascribed to accidental mortality on fishing gear) and low breeding success (averaging 32%, due to mouse predation). Fledgling production from 1979 to 2007 and numbers of incubating adults from 1956 to 2007 have both decreased by ~1% p.a. Consecutive annual counts of incubating adults and a population model permit the first reliable estimates of the Tristan albatross population, presently 5400 breeding adults and 11,300 birds in all age- and stage-classes. Population models explore scenarios of likely demographic trends using combinations of hypothetical best-case estimates vs. observed estimates for two key parameters: adult survival and breeding success. These scenarios highlight the relative benefits to the species of eradicating mice or mitigating bycatch. The model scenario using observed estimates predicts annual growth rate at −2.85%. Adult survival rates have probably decreased in recent years, concomitant with increased longline fishing effort, which might explain the discrepancy between counts and modelled trends. Negative trends cannot be reversed by improving breeding success alone, and adult survival must exceed an improbable 97% to balance the current chick production. A worst-case scenario including a fixed number of adult deaths annually predicted a catastrophic 4.2% p.a. decrease and extinction in ~30 years. Population growth was most sensitive to adult survival, but even using an adult survival estimate without fishery mortality, current breeding success is insufficient to maintain the population. These findings do not support the 'compensatory mitigation of bycatch' model (offsetting bycatch impacts by eradicating invasive species), and the impacts of both fishery mortality and mouse predation must be addressed to improve the conservation status of the Critically Endangered Tristan albatross.

1. Introduction

Island-endemic bird species are amongst the most threatened groups of birds in the world (BirdLife International, 2004). Native birds (and particularly seabirds) are often unable to defend themselves against invasive mammalian predators (Atkinson, 1985; Courchamp et al., 2003; Moors and Atkinson, 1984) that have been introduced to the vast majority of islands around the world (Blackburn et al., 2004; Martins et al., 2006). The problem is often exac-

erbated by small population sizes that are inherently susceptible to extinction (Ebenman et al., 1995; Simberloff, 2000). To illustrate this, the Red List Index shows that seabirds are at significantly higher risk than other birds on average (Butchart et al., 2005). Thus, from a conservation perspective, it is dangerous to be a single-island-endemic seabird species.

Albatrosses have high adult survival, low fecundity and delayed sexual maturity, resulting in limited demographic resilience to lowered adult survival (Croxall et al., 1990; Cuthbert et al., 2004; Weimerskirch et al., 1997; Weimerskirch and Jouventin, 1987). The impact of longline fishing on seabird populations was first recognised in the late 1980s (Brothers, 1991). Thereafter mortality from fishery interactions has been invoked to explain decreases in most Southern Ocean albatrosses, and is still considered their most important conservation threat (Croxall et al., 1990; Cuthbert et al., 2004; de la Mare and Kerry, 1994; Nel et al., 2002a,b; Weimers-

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kirch et al., 1997; Weimerskirch and Jouventin, 1987). Until recently, the only other significant, anthropogenic conservation problem reported currently for Southern Ocean albatrosses is disease, recorded in Indian Yellow-nosed Albatrosses (*Thalassarche carteri*) on Amsterdam Island (Weimerskirch, 2004). In 2007 it was shown that introduced house mice (*Mus musculus*) on Gough Island cause widespread mortality of Tristan albatross chicks (and other seabird species) (Wanless et al., 2007).

The Tristan albatross (*Diomedea dabbenena*) historically bred on Tristan da Cunha, Inaccessible and Gough islands, but humans and their commensal invasive species drove the Tristan da Cunha population extinct (Holdgate, 1965). The Inaccessible Island population has averaged <1 chick per annum since 1982 (Ryan, 2005) and is not considered viable. Gough Island supports >99% of the global population, making the species de facto a single-island endemic. In 2001 a census of breeding Tristan albatrosses on Gough Island was conducted, the first since 1956; evidence of low breeding success (27%) and low adult survival (93%) were also reported (Cuthbert et al., 2004). The consequences of those findings were explored in several scenarios using demographic models, and although few firm conclusions could be drawn, the models generally suggested a population decrease. Here we update Cuthbert et al. (2004) with another 6 years of chick counts, 4 years of counts of incubating birds and breeding success and 3 years of mark-recapture data to reassess the status of the Gough population of Tristan albatross. We refine estimates of recruitment age and adult survival and provide the first reliable estimates of mean annual breeding success, the adult population size and the total population size. The new data allow us to develop a more realistic and robust population model than Cuthbert et al. (2004) were able to achieve, affording greater potential for exploring demographic scenarios. Reinterpretation of historical data in the light of these findings allows a revision of Cuthbert et al.'s (2004) estimate of the annual decrease in the population. Based on this analysis, we confirm the species' Red List status of Critically Endangered. We also demonstrate the relative importance of the conservation actions required to reverse the population trends.

2. Methods

2.1. Estimating population size and breeding success

Tristan albatrosses breed in sheltered areas and on valley slopes above 350 m on Gough Island (40°21'S, 9°53'W), central South Atlantic. Laying peaks in January, hatching in March, and fledging occurs from November onwards (Cuthbert et al., 2004). Counts of Tristan albatross adults (during incubation) and large chicks (prior to fledging) were made by scanning with binoculars from ridge-tops or vantage points. Ryan et al. (2001) showed that scan counts were reliable for Tristan albatrosses on Gough Island. The island is divided into 10 count sectors (Fig. 1). Complete scan counts of incubating adults (January–March) were done in 2001, 2004, 2006 and 2007 and a partial count in 2005. Counts of near-fledging chicks were conducted between September and November, sporadically from 1979 and annually from 1999 to 2007. These counts provide a maximum estimate of the number of chicks produced because further mortality may occur before fledging. However, the absence of fresh Tristan albatross carcasses after October in 2 years of study suggests that mortality from October to fledging is negligible (RMW and RJC, pers. obs.). Incubator and chick counts from the same breeding season allow estimates of the total annual breeding population and maximum breeding success of the population.

Because some annual counts had incomplete spatial coverage (three of 12 chick counts and one of five incubator counts), we esti-

mated values for missing sectors, thereby generating whole-island estimates for years with partial counts. We used a multiplicative model with maximum likelihood estimates, including correction for overdispersion, and estimated expected counts in two-way (site and time) contingency tables (Underhill and Prŷs-Jones, 1994).

We estimated population trends by comparing the 1956 incubating adult counts from Green Hill, Gonydale (including the Hummocks sector) and Albatross Plain, totalling 1130 pairs (see Fig. 1), believed to have been most reliably counted (Cuthbert et al., 2004), to incubator counts in 2004–2007 for the same sectors. We also performed a temporal correlation of chick counts from 1979 to 2007. Differences between chick counts in early (1979–1982) and recent (1999–2007) periods were tested with a Mann–Whitney U test, treating years within each period as independent samples.

It is not possible to determine directly if breeding success in the early period was similar to the present day, because only chick counts were performed before 2001. However, the number of annual breeding attempts can be estimated by dividing the number of chicks by the breeding success. Although this estimate (number of breeding attempts) is dependent on the breeding success estimate used, the vastly different results obtained from using widely differing breeding success estimates provide some insight to the probable value. We used low and high estimates of breeding success (the current mean for Gough Island and 70% breeding success, similar to what has been reported for congeners (Table 1), respectively) to estimate the number of annual breeding pairs in the 1979–1982 period. We then calculated the rates of population change required to move from these two estimates to the present-day (2001–2007) mean and assessed which rate (and thus which level of breeding success) is more likely. Averages were used to minimise potential bias from the inter-annual fluctuations in the number of breeding attempts inherent in a biennially breeding species. The period of change (23.5 years) was calculated from the midpoints of each time-period.

All analyses were performed in Statistica (StatSoft, 2004). Where appropriate, means are reported with one standard deviation (SD), CI denotes 95% confidence intervals and SE denotes standard error.

2.2. Estimating demographic parameters

We developed a female-based, age/stage classified model using the program STELLA to explore the consequences of various scenarios for the mean population growth rate. The following input parameters were estimated: annual juvenile (ages 1–5 years), immature (ages 6–10 years) and adult survival (ages >10 years), annual breeding success, mean recruitment age, probability of failed breeders taking a sabbatical year and the probability of adults taking one or more sabbatical years. Where parameters could not be reliably estimated because data were either lacking or from too few years to be reliable, we used published estimates from congeners as surrogates (e.g. Cuthbert, 2004; Cuthbert et al., 2004; Keitt et al., 2003). For two key parameters (adult survival and breeding success) we used two alternatives: values from normal, healthy populations, derived from congeners (referred to as 'expected') and the actual values estimated from Gough Island (referred to as 'observed'). Expected annual survival was fixed at 0.956, the value used by Cuthbert et al. (2004) and derived from wandering albatrosses *Diomedea exulans* without fishery-related mortality. Expected breeding success was 60–75%, the approximate range reported for congeners (Table 1).

Adult survival, recruitment age and breeding site fidelity were estimated from banding and recovery data from a small study colony on Tafelkop, where adults and chicks have been banded annually since 1985, and the identity of breeding adults recorded. Adult
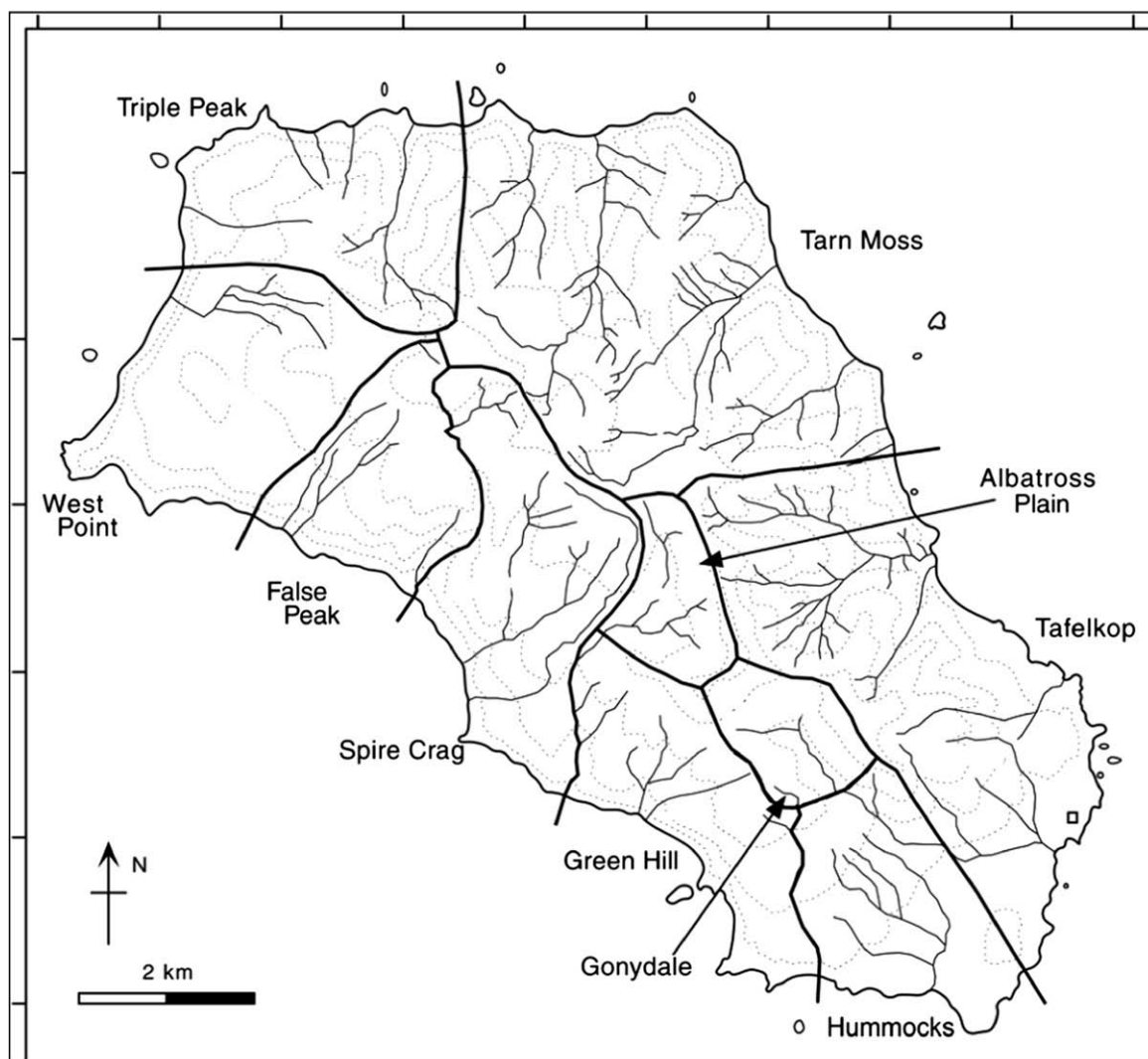
Fig. 1. Count sectors for Tristan albatrosses on Gough Island. Dotted lines indicate contours, thin solid lines represent major water courses and thick solid lines delineate count sectors.

Table 1
Adult survival, breeding success and population growth rates for *Diomedea exulans* (*sensu lato*) albatrosses. All data are percentages and decimals are presented as reported.

Species	Location	Study period	Adult survival	Breeding success	Growth rate (%)
D. [e.] amsterdamensis[a]	Amsterdam	1983–1994	95.7	71.6	+1.0[f]
D. [e.] antipodensis[b]	Antipodes	1994–2004	95.7	74	+1.0
D. [e.] dabbenena	Gough	1985–2006	91.0	32.3	−2.8[f]
D. [e.] exulans[a]	Crozet	1986–1994	95.6	72.0	+1.0
D. [e.] exulans[c]	Macquarie	1955–2000	95.3	–	0
D. [e.] exulans[d]	Marion	1984–1999	94.2	74.6	+5.0
D. [e.] exulans[e]	South Georgia	1961–1988	94	64	−1.0
D. [e.] gibsoni[b]	Auckland	1991–2004	96.1	63	+1.0

[a] Weimerskirch et al. (1997).
[b] Elliott and Walker (2005).
[c] de la Mare and Kerry (1994).
[d] Nel et al. (2003).
[e] Croxall et al. (1990).
[f] Modelled estimate.

survival was estimated using MARK (White and Burnham, 1999). Only birds that bred at least once from 1985 to 2007 were included; retraps of non-breeding birds were ignored. Out of 131 individuals, 63 were retrapped more than twice. Models with time-constant [$\varphi(\cdot)$] and time-variable survival [$\varphi(t)$] were compared. Retrap probabilities (denoted p) were time-variable in both models because sampling effort was, for the most part, reliant on volunteers and varied widely between years (from 0% to >80% of breeders checked for bands). There was zero retrap effort in 2005, so for that year retrap probabilities were zero in all analyses. Model performance was assessed using sample-size adjusted Akaike's Information Criterion (AICc). Observed adult survival

was taken from the MARK model with the lowest AICc. *Diomedea* albatrosses exhibit extremely high fidelity to breeding sites (Cooper and Weimerskirch, 2003; Croxall et al., 1990; Inchausti and Weimerskirch, 2002; Terauds et al., 2006). We could not quantify emigration rates of breeding birds reliably and the apparent emigration rates were too low to merit inclusion in the MARK model. Thus we ignored emigration, so the models slightly underestimated adult survival.

Average recruitment age was estimated from all 40 birds banded as chicks that subsequently bred in the Tafelkop colony. Data were insufficient to analyse only cohorts that have finished recruiting, and retrap effort was variable over the 22 years. These errors produce opposing effects of unknown magnitudes on the estimate; nevertheless, the resultant estimate is similar to that of congeners.

Survival of birds aged 1–5 years (defined as juvenile) and 6 years to first breeding (defined as immature) is unknown for Tristan albatrosses, but we assume the annualised survival of immatures is equal to adult survival, as for congeners (Croxall et al., 1990; Weimerskirch et al., 1997), but see Terauds et al. (2006) for very different adult vs. immature survival rates. Cuthbert et al. (2004) used data from the wandering albatross (*D. exulans*) population on the Crozet Islands (in the Indian Ocean), where annualised survival of juvenile birds was 75.6% (Weimerskirch et al., 1997). However, juvenile survival on South Georgia (in the Atlantic Ocean) up to the 1980s was 81–86% (Croxall et al., 1990). We used the mean of the mid-point South Georgia and Crozet estimates (79.5%, equivalent to 0.837 of adult survival). When modelling observed values, we applied this proportion to the observed (low) annual adult survival value, which generated a concomitant lower annual juvenile survival (76.2%).

The percentage of successful breeders that take a single sabbatical year and the percentage of failed breeders that take a sabbatical year (estimated from congeners) ranged from 72% to 85% and from 22% to 32%, respectively (Croxall et al., 1990; Weimerskirch, 1992). Thus in the model the proportion of non-breeders returning to the breeder stage-class and the proportion of failed breeders returning to the non-breeder stage-class each year were strings of evenly distributed random numbers from 0.72 to 0.85 and from 0.22 to 0.32, respectively.

2.3. Demographic model

The use of stochastic variables that spanned the range of observed/expected values for certain demographic parameters (instead of means as in a deterministic model) allowed a model in which annual variations in breeding success were reflected in the fluctuating numbers of breeding and non-breeding adults, rather than a single, fixed percentage or random variable that was unrelated to breeding success. The model time-step was 1 year and was run for 30 years. It consisted of 13 age- or stage-classes of individuals: two for adults (breeding and non-breeding stage-classes), chicks, five juvenile age-classes (age-classes 1–5 years) and five immature age-classes (age-classes 6–10 years). The model assumed an equal sex ratio and no density-dependent limitations on survival or breeding success. The starting population size for breeders was 2400 females, the 2001 incubator census. Although it is probable that an unusually large number of pairs bred in 2001, this estimate was used to facilitate direct comparisons with Cuthbert et al. (2004). We assumed a stable age distribution and starting population sizes of other classes were derived from a deterministic Leslie matrix model with the same parameters for each combination of parameter alternatives. All values were rounded to the nearest integer during calculations.

Elsewhere, 22–32% of breeders that fail will attempt to breed the following year (Weimerskirch, 1992); the remainder also takes

a sabbatical. This is probably an optimistic estimate for Gough Island, because it is derived from a population where most failures occur during incubation. On Gough Island, most breeding failures occur at the chick-rearing stage (Cuthbert et al., 2004; Wanless et al., 2007), and probably few adults whose attempts fail at this stage have sufficient time to regain condition; thus the annual movement out of the breeder stage-class may be higher than in our model, and the model results should be considered conservative.

We performed sensitivity analyses on the effect that the rate of interchange between the two stage-classes (breeders and non-breeders) had on population growth, because these were surrogate parameters taken from sister taxa. A parameter value was set ±10% of the median value, while keeping all other parameters unchanged (Duplisea, 1998). To illustrate, when testing the model sensitivity to non-breeders returning to breed after a 1-year sabbatical, the median of the estimate is 78.5%, so we tested the effect with this parameter set at a constant, first 88.5% and then 68.5%. The same was then done for failed breeders taking a sabbatical year. Other stochastic variables were made repeatable (i.e. the same string of values was used in each iteration), to allow direct comparisons between simulations. The model's sensitivity to all other parameters was explored in detail in various scenarios, described fully below.

To determine the importance of fishery interactions (affecting adult survival) and mouse predation (affecting productivity) on population trends, four scenarios were simulated using combinations of high (expected) vs. low (observed) values for these two parameters:

Best case: expected adult survival and expected breeding success.

Mouse impacts only: expected adult survival and observed breeding success.

Fishing impacts only: observed adult survival and expected breeding success.

Current case (mouse and fishing impacts): observed adult survival and observed breeding success.

The parameter estimates for adult survival and breeding success implicitly assume that mortality of adults and chicks due to extrinsic threats (fishery interactions and mouse predation, respectively) is proportional to population size. However, the numbers of fishing vessels and longline hooks available to albatrosses are independent of albatross numbers, and it is conceivable that the number of birds killed does not vary in direct proportion to albatross population size, but is relatively fixed in absolute terms – the effect is thus inversely density dependent. We therefore explored the population-level consequences of density-independent, fishery-induced mortality (cf. Ryan et al., 2006) with a further, worst-case scenario, which modelled constant, density-independent adult mortality (to mimic additive, fishery-related mortality) using observed breeding success. If annual adult survival in the absence of fishery mortality is 95.6% (as used in these models) then the observed survival (91.0%) implies that at present 4.4% of adults die as a result of fishery interactions each year. Applying this to the model's estimate of the present-day total Tristan albatross population (ca 5749 females) yielded 253 individuals, which we used as the fixed annual number of albatross deaths – this is within the range of the same estimate made by Cuthbert et al. (2005). The same question (is annual mortality fixed or density dependent) applies to predation. However, *Diomedea* demographics are relatively resilient to minor differences in chick production (Weimerskirch et al., 1997). A scenario of fixed annual chick mortality did not yield results different from those with proportional chick mortality, and consequently we do not present this scenario. For each scenario we calculated the mean population growth rate from 250 iterations.

2.4. Demographic model structure

All model parameters for the various scenarios are presented in Table 2. The breeder stage-class B at time t can be expressed as

$$B_t = B_{(t-1)} \times S + R + W_t - X_t$$

where $B_{t=0}$ is 2400 females, R is recruitment (of immature birds of age-class 10), W is the number of non-breeding birds returning to breed, X is the number of breeders that take a sabbatical year and S is annual survival (a fixed value, not a stochastic variable). The adult non-breeder stage-class D at time t was governed by a simpler subset of conditions, being mortality, gain from X and loss from W, expressed as

$$D_t = D_{(t-1)} \times S + X_t - W_t$$

where $D_{t=0}$ is 1800 females. W_t is the movement of females at time t from D to B, equivalent to the number of non-breeders multiplied by a factor representing the estimated proportion of birds that take a single sabbatical year (72–85%, Weimerskirch, 1992), expressed as

$$W_t = (D_{t-1} \times S) \times Random(0.72, 0.85)$$

where the distribution of random numbers was uniform. X_t is the number of females moving from B to D at time t (i.e. the number taking a sabbatical). This was a function of breeding success (all successful breeders, less those that died, exit B) and the proportion of failed breeders that take a sabbatical year (Weimerskirch (1992) estimated 68–78% of failed birds return the following year), expressed as

$$X_t = B_{t-1} \times S \times P_{t-1} + B_{t-1} \times (1 - P_{t-1}) \times Random(0.22, 0.32)$$

where P is productivity (i.e. breeding success), a stochastic variable that ranged from 0.25 to 0.4 (equivalent to a breeding success of 60–75%, Table 1). The distribution of random numbers was uniform. When modelling the low (observed) estimate of breeding success, the random numbers ranged from 0.55 to 0.73 and the distribution was skewed to produce a mean of 0.68 (i.e. 32%, the mean observed breeding success). Chick production C at time t was purely a function of breeding success and the number of breeding attempts, expressed as

$$C_t = B_t \times P_t$$

Although reproductive success was modelled, the unit for age-class 0 was fledged chicks, not eggs. The juvenile J and immature I populations consisted of 10 age-class stocks Y_n, where n_{1-5} = juveniles and n_{6-10} = immatures. The progression of individuals from one age-class to the next was as follows. At each iteration, each age-class Y_n (for n_{2-10}) at time t was simply Y_{n-1} at time $t-1$ (the previous year's stock), less a mortality factor (S) and the entire C_{t-1} stock became the Y_1 stock. Y_{10} stock (less a mortality factor) exited I to become the recruits R into the breeder stock. Juvenile (Y_{1-5}) survival is lower than immature or adult survival (Cuthbert

Table 3
Initial age-class values for the Tristan albatross demographic model under scenarios with and without mouse impacts on annual chick production.

Age-class	Without	With
Y_1	683	292
Y_2	535	229
Y_3	419	179
Y_4	328	140
Y_5	257	110
Y_6	249	105
Y_7	240	100
Y_8	229	96
Y_9	218	92
Y_{10}	209	88
Total juveniles	2222	950
Total immature	1145	481

et al., 2004) so for these age-classes we multiplied S by a correction factor of 0.837. The age-classes Y_n at time t are described by the following expressions:

$$Y_1 = C_{t-1}$$
$$Y_n = Y_{n-1} - (Y_{n-1} \times S \times 0.837) \quad [1 < n < 6]$$
$$Y_n = Y_{n-1} - (Y_{n-1} \times S) \quad [5 < n < 11]$$

and

$$J_{t=0} = \sum_{t=0} Y_{1-5} = 2222$$

and

$$I_{t=0} = \sum_{t=0} Y_{6-10} = 1145$$

For scenarios which included mouse impacts on chick production, starting population sizes for non-adult age-class were concomitantly lower, with totals of 950 and 481 for J and I, respectively (Table 3).

3. Results

3.1. Estimating population size and breeding success

Whole-island maximum breeding success was ~27% in 2001, 2004 and 2005, 45% in 2006 and 33% in 2007, resulting in a mean success for the period 2001–2007 of 32% (Table 4).

Although more fledglings were produced annually between 1979 and 1982 than during 1999–2007 (Table 4), there was no significant trend over time ($R^2 = 0.17$, $p = 0.183$). However, there was a marked inter-annual oscillation in production in 1999–2000, which damped by 2003–2004. When the 'outlier' years of 1999 and 2000 were excluded, a significant negative correlation was found ($R^2 = 0.61$, $p = 0.008$). A Mann–Whitney U test (adjusted

Table 2
Parameters (per scenario) of a demographic model of the Tristan albatrosses. Mean values are in parentheses.

Parameters varied by scenario	Best case	Mouse impacts	Fishing impacts	Current case	Worst case[a]
Annual survival of adults and age-class 6–10 (%)	95.6	95.6	91	91	95.6
Annual survival age-class 1–5 (%)	79.5	79.5	76.2	76.2	76.2
Stochastic parameters					
Breeding success (%)	60–75 (67.5)	27–45 (32)	60–75 (67.5)	27–45 (32)	27–45 (32)
Failed breeders taking sabbatical (%)	22–32	22–32	22–32	22–32	22–32
Non-breeders returning from 1-year sabbatical (%)	72–85	72–85	72–85	72–85	72–85
Constant parameters					
Successful breeders taking a sabbatical (%)	100	100	100	100	100
Recruitment age (years)	10	10	10	10	10

[a] Included an additional, fixed annual mortality of 253 birds (removed randomly from all age/stage-classes except chicks).

Table 4
Tristan albatross incubator and large-chick counts and maximum annual breeding success estimates from Gough Island. Values in parentheses are estimated totals from partial counts (see Section 2). Extrapolations of the number of incubating pairs from the chick count were done at a breeding success of 32% and 70%.

Year	Incubating pairs	Large chicks	Breeding success (%)	Extrapolation of incubating pairs at 32% success	Extrapolation of incubating pairs at 70% success
1979	–	792	–	2475	1131
1980	–	661	–	2066	944
1982	–	798	–	2494	1140
1999	–	1129	–	3528	1613
2000	–	318	–	994	454
2001	2400	656	27.3	2050	937
2002	–	(463)	–	1447	661
2003	–	(634)	–	1981	906
2004	1869	516	27.6	1613	737
2005	(1939)	(562)	27.3	1756	803
2006	1366	620	45.4	1938	886
2007	1271	610	33.6	1334	610

$Z = 2.39$, $p = 0.017$) confirmed significant differences in annual chick production between the two periods. Mean annual productivity for 1979–1982 ($n = 3$ counts) was 750 chicks, compared to 554 during 2001–2007 ($n = 7$ counts), corresponding to a mean decrease of 1.1% p.a. over 23.5 years. Considering the sectors that we believe were counted reliably in 1956, the incubator counts have decreased 46% over 50 years, from 1130 pairs (1956) to a mean of 607 ± 77 pairs (2004–2007), equivalent to an annual decrease of $0.93 \pm 0.14\%$.

We estimated the number of annual breeding attempts in 1979–1982 by extrapolating back from chick counts. Assuming 70% mean annual breeding success, in 1979–1982 there would have been ~1140 breeding pairs. For that to increase to 1612 pairs, the mean for 2004–2007, requires a growth rate of 1.3% p.a. However, to achieve positive population growth with the observed adult survival estimate for 1985–2007, the model requires an annual breeding success in excess of 100%; thus breeding success even close to 70% in these years is highly improbable. Conversely, assuming 32% breeding success in 1979–1982 yields a mean annual breeding population of 2345 pairs. Forecasting that value to the present requires an annual population growth rate of −1.4% which is similar to the decreasing rate of annual chick production. Working backwards from 1612 pairs at the present at an annual change of 1%, there would have been an average of 2109 incubating pairs in 1979–1982. The breeding success resulting from this figure and the observed chick counts is 37%, within the observed modern range on Gough Island.

3.2. Estimating demographic parameters

The best-fit MARK model had constant adult survival and variable recapture probability over the years 1985–2007, although the time-dependent survival model gave a similar fit ($\varphi(\cdot)$ $p(t)$, AICc = 908.6 vs. $\varphi(t)$ $p(t)$, AICc = 909.7). Mean adult survival was estimated at 0.9096 p.a. (SE ± 0.013, 95% CI = 0.882–0.932) and this was used as the observed adult survival in the population model. The relatively wide confidence limits derive in part from the variable annual retrap effort over the 16 years in which the number of pairs attempting to breed is known. On average 69% (SD ± 27%) of individuals (pairs × 2) were recorded, either as new recruits or as returning breeders in the colony. The mean recruitment age was 10.1 ± 2.7 years (mode 10 years, range 6–20 years, $n = 40$ recruits).

3.3. Demographic model

Not surprisingly, the best-case scenario predicted a stable adult population (average annual growth rate = 0.14%, Table 5, Fig. 2A). The model was not especially sensitive to surrogate parameters, and it is unlikely that any of the surrogate estimates differ widely

Table 5
Estimated annual population growth rates from a 30-year population model for Tristan albatrosses. Worst-case scenario included additional mortality of 253 birds p.a. (taken at random from all age/stage-classes except chicks).

Scenario	Growth rate (%)		
	Mean	Min	Max
Best case	0.14	0.07	0.18
Mouse impacts only	−1.26	−1.32	−1.19
Fishing impacts only	−2.50	−2.56	−2.47
Current case	−2.85	−2.78	−2.91
Worst case	−4.20	−4.33	−4.07

between different *Diomedea* populations. The sensitivity analyses showed the model was relatively robust to changes in the rate at which birds moved between the breeder and non-breeder stage-classes (Table 6).

All other scenarios predicted population decreases. The mouse only model resulted in a population decrease of 1.09% p.a., whereas the fishery only model was more severe, reducing the population by 2.5% p.a. (Table 5). Both survival and breeding success need to improve in order to reverse the model's negative trend. To balance the fishing mortality required the impossible: breeding success >100%, and offsetting mouse predation of chicks requires adult survival to be an unlikely 0.97. Unsurprisingly, the combined impacts of fishing mortality and predatory mice predicted the lowest annual growth rate (−2.85% p.a.). Under this scenario, the Gough population will be reduced to 385 ± 20 breeding attempts p.a. within 30 years (Fig. 2B).

The mean number of pairs attempting to breed from 2004 to 2007 was 1612. The closest value to this in the current-case scenario was 1514 breeding pairs (in 2008). In this year the mean ($n = 250$ iterations) total female population (birds of all age- and stage-classes, including fledged chicks of the year) was 5743 and the total breeding female population was 2746 birds (total population and total breeding population were *ca* 11,300 birds and *ca* 5400 birds, respectively).

Fig. 2C shows that when significant, density-independent juvenile, immature and adult mortality (from fishery interactions in this case) were modelled, the population underwent very rapid decreases. Extinction occurred always within 29 years and in 31 iterations it came as early as in 24 years. Thus if mortality from fisheries is indeed density independent and occurs annually at modelled rates, time to extinction of *ca* 30 years should be considered a fairly realistic estimate.

4. Discussion

All the available data indicate that the Tristan albatross population has been decreasing since at least the 1980s. First, estimates of
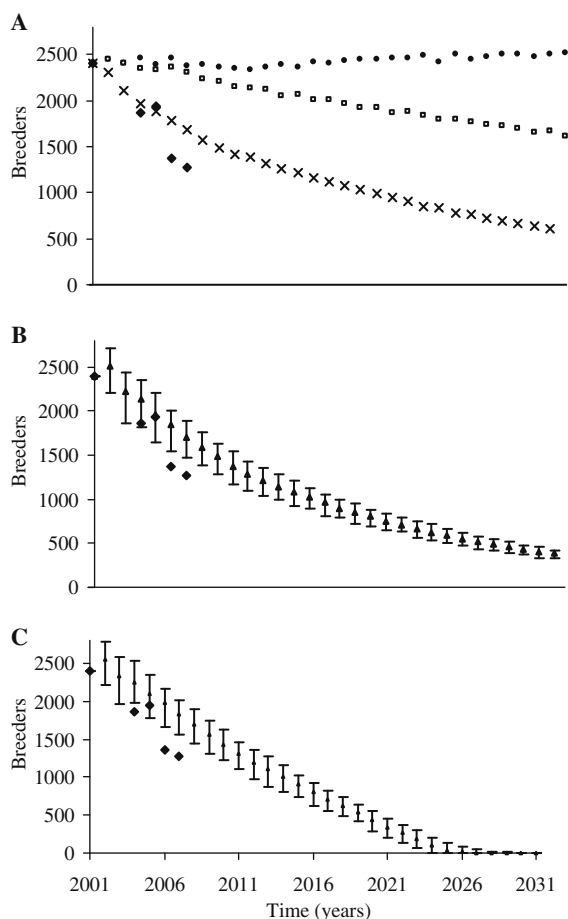
Fig. 2. Mean growth rates in numbers of annual breeding females (from 250 iterations) from a 30-year model of the female Tristan albatross population on Gough Island, starting with the incubator count in 2001. Vertical bars denote 95% confidence intervals (omitted from (A) for legibility) and ♦ = actual incubator counts. Results of scenarios where proportional mortality was modelled are (A) ● = best case (high survival and high annual productivity), □ = mouse impacts only (high survival and low annual productivity), × = fishing impacts only (low survival and high annual productivity) and (B) the current case (low survival and low annual productivity). (C) Shows results of a worst-case scenario, with fixed post-fledging mortality of 253 individuals per year (=additive mortality e.g. from fishery interactions) affecting all post-fledging stages and using observed breeding success.

count was probably high due to an unbalanced demi-population (linked to unusually large numbers of fledglings in 1999 sending a large proportion of the population on sabbatical, which then returned to breed again in 2001).

The best-case scenario, which used adult survival and breeding success estimates close to those of other *Diomedea* populations, produced a very similar estimate of annual growth to those of other populations (Table 1). This suggests that the basic assumptions and workings of the model were reasonable. Although Weimerskirch et al. (1997) argued correctly that a 5% decrease in average breeding success in the wandering albatross would have a negligible impact on population growth, Cuthbert et al. (2004) showed that an average decrease of >20% was sufficient to cause negative population growth for Tristan albatrosses, a finding supported here. Tristan albatrosses are killed during fishing operations (Cuthbert et al., 2005; Glass et al., 2000; Neves et al., 2006; Ryan et al., 2001), and it is quite possible that fishery-related mortality is roughly constant, rather than proportional to the population. Modelling this in the worst-case scenario compounded the effect of low observed adult survival such that the proportional loss of adults (and thus the rate of decrease in adult survival) accelerated over time. In presenting the results of this scenario (extinction by as early as 2025, annual growth rate −4.2%), we do not wish to be alarmist. Presumably the true situation is somewhere between the strictly proportional and additive adult mortality models.

Cuthbert et al. (2004) presented the first whole-island count of incubating Tristan albatrosses since 1956 and the first data on breeding success for the whole of Gough Island. However, the paper relied on a single year of data for some key aspects, and could not define others, such as the regularity of low breeding success or size of the non-breeding part of the demi-population. The demi-population was strongly asymmetric from 1999 to 2002 as a result of apparently high breeding success in 1999 (large fledgling count; Ryan et al., 2001), making inference particularly difficult. Table 7 summarises the key findings of this study relative to those reported in 2004. The updated information suggests a worse outlook for the species' demography.

Our data confirm that low breeding success, a result of mouse predation (Wanless et al., 2007), is the current norm for Tristan albatrosses on Gough Island. How long have mice been attacking albatross chicks and causing widespread reproductive failure? Using likely population growth rates and back-calculations from chick counts in 1979–1982, we conclude that breeding success has been similar to the present, abnormally low levels since at least the late 1970s. There is intriguing circumstantial evidence that mice have caused widespread and large-scale reproductive failure from at least the 1880s.

Mice were probably introduced to Gough Island by early sealing parties, most likely in 1810/1811 (Wace, 1961). The earliest biological report of Gough Island includes the following description: "not more than five out of a hundred [Tristan albatross chicks] live to leave their nests. They are killed by [Subantarctic Skuas *Catharacta antarctica* and giant-petrels *Macronectes* spp.]" (G. Comer, as cited by Verrill, 1895, p. 437). Comer most likely observed skuas and

breeding success from recent years are much lower than has been reported for congeners without chick predators (Croxall et al., 1990; Elliott and Walker, 2005; Walker and Elliott, 2005; Weimerskirch et al., 1997; Weimerskirch and Jouventin, 1987) and are sufficiently low to cause a long-term population decrease. Second, recent (2004–2007) annual fledgling production is lower than it was in 1979–1982. Third, the trend in the five incubator counts this decade is downward, with *ca 1200* (50%) fewer incubating adults counted in 2007 than in 2001 (Table 4), although the 2001

Table 6

Sensitivity of a Tristan albatross demographic model to two parameter estimates taken from congeners. In the default model, these parameters were stochastic, but for the sensitivity analysis (SA) they were made, in turn, a constant value ±10% of the median. For all other parameter values see Table 2 "best case" and for comparison with default model growth rates see Table 5 "best case".

Parameter	Value for SA	Growth rate (%)		
		Mean	Min	Max
Non-breeders returning from 1-year sabbatical (%)	88.5	0.18	0.14	0.26
Non-breeders returning from 1-year sabbatical (%)	68.5	0.11	0.05	0.18
Failed breeders taking sabbatical (%)	17	0.28	0.23	0.33
Failed breeders taking sabbatical (%)	37	−0.14	−0.19	−0.09

Table 7
Key demographic parameters for the Tristan albatross at Gough Island. Values in parentheses indicate number of years of data.

Parameter	This study
Annual adult survival[a] (21)	91.0%
Mean breeding success (5)	32%
Mean recruitment age (21)	10.1 years
Total adult population[a] (2004–2006)	5400
Total population[a] (2004–2006)	11,300
Annual population growth[a]	−2.85%
Estimated annual growth rate since 1956	−0.92%

[a] Modelled.

giant-petrels scavenging carcasses or attacking moribund or fatally wounded chicks by daylight (as is still the case nowadays) and predictably deduced that the predatory birds were responsible. This is at odds with our current understanding of albatross chicks' vulnerability to avian predators (attacks by these species on healthy albatross chicks are exceptionally rare); reinterpretation of Comer's observation suggests that mice have been preying upon Tristan albatross chicks at levels that would have had measurable effects on population growth rates for more than a century.

The apparent annual rate of decrease in number of breeding attempts from 1956 to the present (0.9%) is close to the rate of decrease in annual chick production from 1979–1982 to the present (1.1%). These are similar to the rate predicted in the mouse-only impacts scenario, but contrast with the (considerably larger) decrease in the current-case scenario. This contrast is probably due to the fact that the demographic model uses a mean estimate of adult survival from 1985 to 2007, whereas the reality is that it changes annually. Fisheries are unlikely to have had a significant effect on adult survival before the 1970s, and probably had their most severe effect in the 1990s, possibly extending into this millennium (Tuck et al., 2003). A second source of error in the estimates relates to the lack of reliable counts of incubating adults prior to 2001. The results of this study were used to reclassify the Tristan albatross from Endangered to Critically Endangered (under criterion B1 *a* + *b*, BirdLife International, 2004). This designation depends on the assumption that the population model provides the most appropriate method of inferring current and future population trends, given that the time-period of counts of incubating adults is too short for a clear assessment.

If the benchmark 1956 count was indeed an underestimate, it has had an ironic negative consequence for Tristan albatross conservation on Gough Island. First, from 1957 to 2000 no ornithologist over-wintered on Gough Island and all albatross censuses for that period were chick counts in the austral spring. Table 4 reveals a perverse coincidence: assumptions of normal breeding success before 2001 meant that hindcasting from chick counts to numbers of pairs match closely the 1956 (under)estimate of breeding pairs. Second, counting Tristan albatrosses with binoculars from vantage points is extremely unlikely to result in observers detecting wounds on chicks. As a consequence, widespread and devastating mouse attacks on Tristan albatross chicks have, until very recently, gone unnoticed (Ryan et al., 2001) or unconfirmed (Cuthbert and Hilton, 2004; Cuthbert et al., 2004). These attacks have almost certainly been happening since at least the 1970s and quite likely since before 1888 (Verrill, 1895), and have probably contributed significantly to an estimated 50% decrease in the breeding population over 50 years, and are one of the most pressing conservation issues affecting an albatross species since the impacts of fishery interactions were described (Brothers, 1991).

Reduced adult survival is likely to have commenced with the increase in fishing effort in the Atlantic and Indian oceans that began in the 1970s and continues to the present day (Cuthbert et al.,

2005; Glass et al., 2000; Ryan et al., 2001; Tuck et al., 2003). The population models presented here, however, show that observed low adult survival probably has a stronger negative effect on population growth than observed low productivity levels. This is in direct contrast to the 'compensatory mitigation' conservation model mooted as a solution to bycatch mortality (Wilcox and Donlan, 2007). In that model, eradication of invasive species is used to offset losses to fishery bycatch, and is funded by fining the fishery rather than imposing closures. For a thorough critique, see Finkelstein et al. (2008). Irrespective of the relative impacts, the Tristan albatross population on Gough Island, the last viable population of this species in the world, will continue its apparent trend towards extinction unless the negative effects of both low chick production (from mouse attacks) and low adult survival (from fishery interactions) are ameliorated. Several positive steps have already been taken towards managing the impacts of mice. A recent assessment of the feasibility of eradication of mice from Gough Island concluded that, with some caveats, there were no insurmountable technical barriers to a successful operation (Parkes, in press). Second, the Tristan Island Council has approved the principle of such an action (D. Morley, in litt.). Third, a pilot study of bait acceptance by mice on Gough Island showed that mice were highly motivated to accept baits (Wanless et al., 2008), and a larger study is now planned to determine if 100% bait acceptance can be achieved. We are encouraged by the global attention that incidental mortality of albatrosses (and other non-target species) from longline fishing continues to receive, and support calls for better monitoring, reporting and regulation of fisheries that kill seabirds, including vessels operating on the high seas.

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