



The anatomy of a (potential) disaster: Volcanoes, behavior, and population viability of the short-tailed albatross (*Phoebastria albatrus*)

M.E. Finkelstein^{a,*}, S. Wolf^a, M. Goldman^a, D.F. Doak^b, P.R. Sievert^c, G. Balogh^d, H. Hasegawa^e

^a Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA 95064, USA

^b Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA

^c US Geological Survey, Massachusetts Cooperative Fish and Wildlife Research Unit, University of Massachusetts Amherst, Amherst, MA 01003, USA

^d US Fish and Wildlife Service, Endangered Species Program, Anchorage, AK 99501, USA

^e Biology Department, Toho University, Chiba 274-8510, Japan

ARTICLE INFO

Article history:

Received 19 June 2009

Received in revised form 14 October 2009

Accepted 20 October 2009

Available online 26 November 2009

Keywords:

Albatross

Catastrophe

Chronic

Disaster

Population viability analysis

Stochastic

Volcano

ABSTRACT

Catastrophic events, either from natural (e.g., hurricane) or human-induced (e.g., forest clear-cut) processes, are a well-known threat to wild populations. However, our lack of knowledge about population-level effects of catastrophic events has inhibited the careful examination of how catastrophes affect population growth and persistence. For the critically endangered short-tailed albatross (*Phoebastria albatrus*), episodic volcanic eruptions are considered a serious catastrophic threat since approximately 80% of the global population of ~2500 birds (in 2006) currently breeds on an active volcano, Torishima Island. We evaluated how short-tailed albatross population persistence is affected by the catastrophic threat of a volcanic eruption relative to chronic threats. We also provide an example for overcoming the seemingly overwhelming problems created by modelling the population dynamics of a species with limited demographic data by incorporating uncertainty in our analysis. As such, we constructed a stochastic age-based matrix model that incorporated both catastrophic mortality due to volcanic eruptions and chronic mortality from several potential sources (e.g., contaminant exposure, fisheries bycatch) to determine the relative effects of these two types of threats on short-tailed albatross population growth and persistence. Modest increases (1%) in chronic (annual) mortality had a 2.5-fold greater effect on predicted short-tailed albatross stochastic population growth rate (λ) than did the occurrence of periodic volcanic eruptions that follow historic eruption frequencies (annual probability of eruption 2.2%). Our work demonstrates that periodic catastrophic volcanic eruptions, despite their dramatic nature, are less likely to affect the population viability and recovery of short-tailed albatross than low-level chronic mortality.

© 2009 Elsevier Ltd. All rights reserved.

1. Introduction

Wild species are affected by multiple threats, both natural (e.g., drought, floods) and anthropogenic (e.g., habitat destruction, over-harvesting). Threats can also be divided into those that occur at different frequencies and intensities: (a) chronic threats – constant and often low in intensity (e.g., harvesting); (b) stochastic threats – erratic and unpredictable and of low to moderate intensity (e.g., weather effects); and (c) catastrophic threats – rare, often unpredictable, and of high intensity (e.g., hurricane). Although much work has evaluated the effects of chronic and stochastic threats on population viability (Baker and Wise, 2005; Inchausti

and Weimerskirch, 2001; Kelly and Durant, 2000; Nantel et al., 1996; Rolland et al., 2009), less is understood about how catastrophic threats affect population persistence, especially when combined with chronic and stochastic threats (McCarthy, 1996; Whitman et al., 2007).

While there are multiple ways to assess how catastrophic and/or chronic events might affect species survival, population viability analysis provides one of the most useful approaches, at least when sufficient census and demographic data are available (Morris and Doak, 2002). Population viability analyses (PVAs) are mathematical models based on existing data (e.g., population monitoring, demographic) that predict population growth rates and extinction risks over a specified time frame (Caswell, 2001; Morris and Doak, 2002). PVAs are useful in diagnosing population trends and have been used widely to assess the effect of chronic threats (e.g., bycatch, human disturbance) on the survival of imperilled species (Crowder et al., 1994; Gerrodette and Gilmartin, 1990; Lewison

* Corresponding author. Address: Department of Microbiology and Environmental Toxicology, University of California, Santa Cruz, CA 95064, USA. Tel.: +831 459 4571; fax: +831 459 3524.

E-mail address: myraf@ucsc.edu (M.E. Finkelstein).

et al., 2004b). In contrast, catastrophic threats are commonly omitted from PVAs due to lack of information on their frequency and severity (Coulson et al., 2001; Nilsson, 2004), yet are also believed important with respect to population persistence (Coulson et al., 2001; Ludwig, 1999; Mangel and Tier, 1994).

The general concept that catastrophes significantly affect population persistence may indeed have come from the observation that a catastrophic event can cause dramatic short-term population declines, either from direct mortality or breeding failure. However, many species have life history strategies that buffer them from the effects of catastrophes, especially naturally reoccurring events such as fire, hurricanes, and floods (Breininger et al., 1999; Hughes, 1994; Tryjanowski et al., 2009). Unfortunately, when populations are also affected by chronic mortality (e.g., harvesting), their ability to recover from a catastrophe is inhibited (Hughes, 1994; Whitman et al., 2007). This is particularly true if a population has already been reduced to a small size (Marmontel et al., 1997; Oli et al., 2001; Root, 1998). Thus, including catastrophic effects is important, especially for small populations, to accurately assess a population's future growth and stability (Gerber and Hilborn, 2001; Good et al., 2008).

While others have investigated the theoretical effects of catastrophes and/or chronic mortality on populations (Abrams, 2002; Hanson and Tuckwell, 1981; Lande, 1993), we examined how a real-world catastrophic threat, a volcanic eruption, in combination with and relative to chronic threats affect the recovery of a critically endangered species, the short-tailed albatross (*Phoebastria albatrus*). The short-tailed albatross is the largest North Pacific seabird and, similar to other albatross species, is long-lived, slow to mature, has low annual fecundity, and forages over vast oceanographic regions (Suryan et al., 2007; Tickell, 2000). The short-tailed albatross was listed as endangered in 1970 (USFWS, 2005) due in large part to their near extinction in the 1940s from feather hunting (Austin, 1949; Sanger, 1972). While short-tailed albatross numbers have steadily increased since 1947 (Austin, 1949), there were only ~2500 individuals in 2006 and current threats, both catastrophic and chronic, still appear to jeopardize their recovery.

The catastrophic threat to short-tailed albatross occurs on Torishima (30° 29'N, 140° 19'E), an active volcanic island where the vast majority of the world's population breeds (Hasegawa and DeGange, 1982). Torishima has experienced three above-ground eruptions over the past 130 years, in 1902, 1939, and 2002 (data set available online, <http://www.volcano.si.edu/world/volcano.cfm?vnum=0804-09=&volpage=erupt>; Kuno, 1962), all of which occurred outside of the breeding season. The risk of a volcanic eruption occurring during the breeding season, when the birds are present on the island, has been cited as a major threat to short-tailed albatross given that an eruption could lead to catastrophic adult and chick mortality as well as destruction of nesting habitat (USFWS, 2005). Additionally, short-tailed albatross may be at risk from chronic threats such as fisheries bycatch (Anonymous, 1999) and contaminant exposure (Kunisue et al., 2006), both of which are considered serious threats for another North Pacific seabird, the black-footed albatross (*Phoebastria nigripes*) (Auman et al., 1997; Finkelstein et al., 2007; Lewison and Crowder, 2003).

To examine the relative effects of chronic and catastrophic threats on the population viability of short-tailed albatross, we constructed a series of age-based stochastic population models. Similar to the work of Hunter et al. (2000) on short-tailed shearwaters (*Puffinus tenuirostris*), we paid special attention to the problems of parameter uncertainty as we borrowed data from several albatross species to fill gaps in our knowledge of short-tailed albatross demography. Our work is among the first efforts to provide a comprehensive assessment of the relative population-level effects of a well-defined catastrophic event and low-level chronic mortality for an endangered species. Additionally, we provide an example

for overcoming the seemingly overwhelming problems created by modelling the population dynamics of a species with limited demographic data by illustrating a strategy to account for uncertainty in vital rate estimates.

2. Materials and methods

2.1. Basic model structure

2.1.1. Matrix

The stochastic simulations were based on a 14-stage Lefkovich matrix that includes both males and females grouped together into four juvenile age classes, four sub-adult age classes, one adult stage class, and five adult widow stage classes (in which a bird has lost its mate) (Fig. 1, Table 1). Males and females are assumed to have equal demographic rates. Each year of the model begins in October when adults return to the island to lay eggs and follows birds and their young through September of the next year. The first juvenile age class spans the one-year-old to two-year-old age category (note that the transition from an egg to a one-year-old bird is included in the fecundity term (Fig. 1)), and age classes continue in 1 year increments through 8 years of age, after which birds are considered to be mature breeding adults. Birds aged nine and older were assigned to the adult age class because field data indicate that all short-tailed albatross have attempted to breed at least once by age nine (H. Hasegawa, unpublished data). Similar to others who have modelled albatross populations (Arnold et al., 2006; Lewison and Crowder, 2003; Weimerskirch et al., 1997), we did not incorporate senescence as there is limited empirical evidence for senescence in any albatross species and none to suggest senescence occurs in short-tailed albatross.

2.1.2. Widow classes

A volcanic eruption could potentially kill all short-tailed albatross present on the island. As both members of an albatross breeding pair alternate egg incubation and chick rearing duties (Tickell,

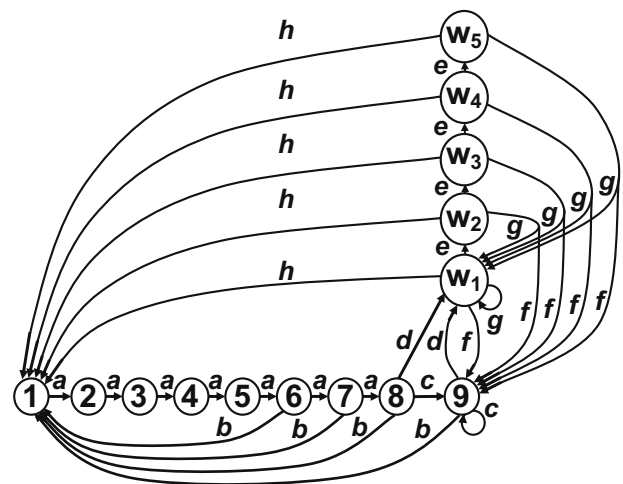


Fig. 1. Diagram of stage-based model developed for short-tailed albatross (see also Table 1). Numbers in circles indicate age or stage classes (1–9) and w_1 – w_5 are widowed birds in the 1st through 5th year since widowhood. Letters associated with each group of transition arrows indicate the types of transitions: (a) the probability of surviving (S_i), (b) fecundity; the probability of producing a viable one-year old in the next generation ($f * b_i * S_C * S_{fledge}$), (c) the probability of surviving and not being widowed ($S_i * (1 - S_i)$), (d) the probability of surviving and being widowed ($S_i * (1 - w_i)$), (e) the probability of a widow surviving and not finding a new mate ($S_i * (1 - w_i)$), (f) the probability of a widow surviving and finding a new mate ($S_i * S_i * w_i$), (g) the probability of a widow surviving, finding a new mate and being widowed again ($S_i * (1 - S_i) * w_i$), (h) fecundity; the probability of a widow finding a new mate and successfully producing a one-year old in the next generation ($w_i * f * b_i * S_C * S_{fledge}$).

Table 1

Short-tailed albatross population matrix used for model simulations. $N_{i,t}$ is the age specific population size at time t , S_i is the age specific survival, w_i is the probability of finding a mate after being widowed (note in year 5 (w_5) the probability of finding a mate is 100%) and F is fecundity, the probability of producing a viable one-year old in the next generation and defined as the following:

$$F_{1..4} = f \times b_i \times S_{c_i} \times S_{fledge}$$

$$F_{5..9} = f \times b_i \times S_{c_i} \times S_{fledge} \times w_i$$

where f is the proportion of the population that is female (assumed to be 0.5), b_i is the probability of breeding for i aged birds, S_{c_i} is the survival of chicks raised by an i aged female parent from egg to fledge (6 months), and S_{fledge} is the probability of surviving from fledge to 1-year old (6 months).

	0	0	0	0	0	F_1	F_2	F_3	F_4	F_5	F_6	F_7	F_8	F_9
$N_{i,t}$	S_i	0	0	0	0	0	0	0	0	0	0	0	0	0
	0	S_i	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	S_i	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	S_i	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	S_i	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	S_i	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	$(S_i)^2$	$(S_i)^2$	$(S_i)^2 w_i$	$(S_i)^2 w_i$	$(S_i)^2 w_i$	$(S_i)^2 w_i$	$(S_i)^2 w_i$
	0	0	0	0	0	0	0	$S_i(1 - S_i)$	$S_i(1 - S_i)$	$S_i(1 - S_i)w_i$	$S_i(1 - S_i)w_i$	$S_i(1 - S_i)w_i$	$S_i(1 - S_i)w_i$	$S_i(1 - S_i)w_i$
	0	0	0	0	0	0	0	0	$S_i(1 - w_i)$	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	$S_i(1 - w_i)$	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	$S_i(1 - w_i)$	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	$S_i(1 - w_i)$	0	0

2000), one mate from all breeding pairs may be simultaneously killed if a volcanic eruption occurs during the breeding season. The concurrent death of one member from all breeding pairs may affect short-tailed albatross population dynamics through the 1–5 year time lag required for widowed mates to find a new breeding partner (Fisher, 1976). Consequently, in order to account for changes in population dynamics from widowing effects, breeding birds that were widowed (due to any mortality event) were transitioned from the breeding age class into a non-breeding widow class. By transitioning birds annually through five widow classes, the model allowed the probability of a bird finding a new mate to increase with time since that bird was widowed (annual probability of finding a mate after being widowed: year 1 = 1%, year 2 = 59%, year 3 = 63%, year 4 = 60%, year 5 = 100% based on data for Laysan albatross in Fisher (1976)). Note that in year 5 all widowed birds were assumed to find a mate (Fisher, 1976).

2.1.3. Density dependence

Similar to a recently published model on short-tailed albatross population dynamics (Zador et al., 2008), density dependence was not incorporated into our model structure. The global short-tailed albatross population has been steadily increasing from near extinction since the early 20th century (Austin, 1949); recent census data (1976/77–2005/06) provide no indication that Allee effects are operating as evidenced by a constant lambda (variance = 0.002) with a growth rate (1.073) higher than that observed for other albatross species (Appendix A). Nor is negative density dependence likely affecting this population as the current population size (~2500 birds in 2006) is orders of magnitude lower than the population size prior to feather hunting (Austin, 1949).

2.1.4. Migration

We did not incorporate migration into our model structure as typically only one bird believed to be from the Senkaku islands – the only other established Short-tailed albatross colony – is seen on Torishima each year and there is no evidence that these birds are breeding (P. Sievert, pers. obs. 2007). Very little is known about albatross movement rates between breeding colonies although

rates are thought to decline with increased distance and juveniles appear to be the most likely age group to disperse (Inchausti and Weimerskirch, 2002). In general, migration is not considered an important driver for albatross population dynamics as adults have strong nest site fidelity, returning to the same nest to breed year after year, and their chicks tend to recruit as breeders to the same colony where they were raised (Tickell, 2000).

2.2. Parameter estimates

2.2.1. Uncertain parameters: demographic rates estimated from other albatross species

While census data (e.g., numbers of eggs laid, chicks fledged each year, age of first breeding) exist from Torishima between the years 1976/77–2005/06, no other demographic data were available for short-tailed albatross. Thus, models were constructed, with the incorporation of uncertainty, using estimates of survivorship and probability of breeding from a wide range of albatross species (see Appendix A) as there was no evidence to indicate that any one species (or groups of species) would be more representative of short-tailed albatross population dynamics.

2.2.1.1. Mean rates. For each vital rate not based on short-tailed albatross demography, sets of three to five plausible (with respect to the observed growth rate from census data), mean values were selected based on mean rates reported for other albatross species (Table 2, see Appendix A). Younger birds (ages six to seven) were assigned lower probabilities of breeding compared to older birds (ages 8 and above) (Table 2). Our breeding probability values were slightly higher than those of other albatross species (Appendix A) since: (1) high rates were necessitated by the observed high growth rate of the population (1.073) and (2) widowed birds were partitioned out of the adult stage class such that probability of breeding values applied only to adults with the potential to breed.

To run each simulated population trajectory, we selected a particular set of mean survival and mean breeding probability rates from the 1500 possible vital rate combinations. In lieu of randomly picking a set of vital rates to use, we took a more targeted approach

Table 2

Vital rate means, variances, and bounds used in short-tailed albatross stochastic model simulations. Vital rates with more than one mean are those for which no short-tailed albatross-specific demographic data were available (see Appendix A for the data upon which these rates are based). A set of vital rates was picked for each model simulation by their relative likelihood of obtaining the census-calculated lambda (1.073). To incorporate environmental stochasticity, a value was randomly selected every year from a beta distribution that was constructed with the mean being the vital rate selected for each simulation and the annual variance (which remained constant for all simulations). Bounds were set on the beta distributions for probability of breeding rates to ensure realistic values were chosen as these rates have a large estimated variance.

Vital rate	Mean (s)	Variance	Bounds
Survival: egg to fledge	0.551	0.015	–
Annual survival: immature (fledge to 4)	0.88, 0.89, 0.9, 0.91, 0.92	0.003	–
Annual survival: sub-adult (5–8)	0.94, 0.95, 0.96, 0.97	0.001	–
Annual survival: adult (9+)	0.96, 0.97, 0.98	0.0005	–
Annual probability of breeding: sub-adult	0.51, 0.53, 0.55, 0.57, 0.59	0.014	0.1–0.7
Annual probability of breeding: adult	0.84, 0.86, 0.88, 0.9, 0.92	0.014	0.45–0.95

by evaluating how closely each individual vital rate set, when used in the stochastic model, would approximate the growth rate (lambda) of 1.073, calculated from census data on Torishima between the years 1976/77–2005/06. To do this, 500 stochastic simulations were run for 30 years using each of the 1500 vital rate sets, thereby generating a mean and standard deviation of the stochastic lambda for each set. We estimated the likelihood of obtaining the observed, census-calculated lambda (1.073) from each vital rate set, assuming normally distributed lambda values. We then randomly picked 1000 vital rate sets for use in our model simulations, weighting the choice of these sets by their relative likelihood of obtaining the census-calculated lambda (1.073). To determine whether 1000 vital rate sets were sufficient to generate consistent and reproducible results, we chose two different groups of 1000 sets and found that the mean and variance of the predicted stochastic lambda values changed by less than 0.03%.

2.2.1.2. Vital rate variances. The temporal annual variance in survivorships and probability of breeding were estimated using the mean value of the variance estimates for each rate reported for other albatross species (see Appendix A). When possible, we used variance estimates that appeared to be corrected for sampling variance. However, the majority of studies in the literature do not correct for sampling variance or provide the information needed for us to make these corrections. Nonetheless, given that the mean survival estimates from all studies evaluated are extremely high and the variances are very small (see Appendix A), incorporation of some estimates that reflected total variance (and not solely process variance) should not significantly affect our findings. The average of variance estimates reported for other albatross species, $\bar{\sigma}^2$, was then rescaled to yield the proportion of the maximum variance possible for a rate with the mean of the relevant survival estimates (\bar{v}): $p = (\bar{\sigma}^2 / (\bar{v} * (1 - \bar{v})))$ (Morris and Doak, 2002). Temporal variances used in model simulations (Table 2) were then calculated by multiplying p by $\bar{v}_i(1 - \bar{v}_i)$, where \bar{v}_i is the vital rate mean of the 1000 vital rates (from selected vital rate sets, see above). As all estimates of temporal variance were very low (see Appendix A), and there was a narrow range of mean values (and hence low uncertainty in the means), this approach was adequate to estimate reasonable temporal variance values. Parameter uncertainty for vital rate variances was not included in our simulations: (1) because the high growth rate dictated that mean rates (survivorship rates in particular) could not be highly variable between years; (2) a preliminary assessment of including parameter uncertainty in vital rate variances (following the same methodology used for the parameter means), negligibly altered the annual variance in lambda (0.0023–0.0027).

2.2.2. Parameters based on short-tailed albatross demographic data

2.2.2.1. Survivorship values. The mean and the variance of egg to fledging survivorship (0.551 and 0.015, respectively) was calcu-

lated using short-tailed albatross field data for 1976/77–2005/06 (H. Hasegawa, unpublished data).

2.2.2.2. Age of first breeding. Age of first breeding was set at 6 years based on short-tailed albatross re-sighting data from Torishima where chicks banded in 1988, 1989, and 1990 were re-sighted as breeders over the next 10 years. Only a small percentage of re-sighted birds (13%) began breeding at age five compared with 42% at age six (H. Hasegawa, unpublished data).

2.2.2.3. Population sizes. The starting population size in all model simulations was 1485 birds and the population was assumed to be at a stable stage distribution. The starting population size was estimated by first calculating the number of breeding adults (682) as a result of doubling the number of eggs observed in Autumn 2006 (341 eggs, H. Hasegawa, unpublished data). Then, the stable age distribution was calculated using vital rates from the vital rate mean sets (Table 2) that resulted in a lambda (1.074) which closely approximated the lambda generated from the census data (1.073) as follows: probability of breeding for 6 and 7 year olds = 0.55, probability of breeding for 8 and older = 0.88, immature survival (fledge to 4) = 0.90, sub-adult survival (5–8) = 0.96, and adult survival (9+) = 0.98. The number of breeding birds, the stable age distribution, and the probability of breeding were used to estimate the total population size.

Extinction was said to have occurred when the population hit the quasi-extinction threshold of 100 adults, ages eight and above, including widowed birds. One Hundred breeding adults was chosen as this number equals an effective population size of 50 individuals, which results in the loss of ~1% of genetic diversity each generation – a loss generally considered low enough to minimize negative effects such as inbreeding depression (Morris and Doak, 2002). However, for short-tailed albatross, a quasi-extinction threshold of 100 adults may be conservative given their ongoing recovery from near extinction in the early 20th century (Austin, 1949), when population numbers may have fallen below 100 breeding-age adults.

2.3. Simulating environmental stochasticity

Environmental stochasticity was incorporated for stage-specific survivorship and probability of breeding rates. For each of these rates, a value was randomly selected every year from a beta distribution that was constructed with the mean being the vital rate selected for each simulation (from the 1000 vital rate sets) and the annual variance (which remained constant for all simulations, Table 2). Additionally, to ensure that no unrealistic values were selected for annual probability of breeding (given the large variance in these rates), the annual probability of breeding beta distributions were bounded between 10–70% for birds 6–7 years old and 45–95% for birds eight and older (Table 2) in all stochastic simulations.

2.4. Model validation

The fit of the stochastic model, including uncertainty in demographic parameters, was validated by comparing the observed number of eggs each year on Torishima between 1976 and 2006 to the projected number of eggs by running the model for 30 years, at the starting population size in 1976, for 1000 simulations. The mean Pearson correlation coefficient of 0.96 (SE: 0.0006) showed a very close fit of the model projections to the census egg data. Additionally, there was good agreement between the variance in annual lambda values from the field data (0.0022) and those from the model simulations (0.0016).

2.5. Threats to short-tailed albatross

2.5.1. Catastrophic volcanic eruption

Approximately 80% of the short-tailed albatross population nests on the active volcano, Torishima. Torishima has experienced three somewhat consistently spaced above-ground eruptions since 1871 (1902, 1939, 2002) (<http://www.volcano.si.edu/world/volcano.cfm?vnum=0804-09=&volpage=erupt>; Kuno, 1962). Thus, the probability of an eruption occurring each year was assumed to be 2.2% (the three recorded eruptions occurred over 136 years of observation (1871–2007)). In the event of an eruption, the eruption was randomly assigned to occur in a particular month of the year. The probability that a bird in each age class would be present on the island during a particular month of the eight-month breeding season (October–May) was based on attendance data from Laysan albatross, which have a similar breeding cycle (Fisher and Fisher, 1969, see Appendix B). Note that for Laysan albatross the courting and copulation period for a breeding pair is, in general, extremely short (less than three days) (Fisher and Fisher, 1969). For example, Fisher and Fisher (1969) observed that copulation typically occurs within hours after the reunion of mates on the colony and that both birds leave the colony within 36 h after copulation. Thus, as we integrated colony attendance over a one-month period, we did not consider a scenario where both members of a breeding pair would be present simultaneously on the island in our model simulations. In addition, each member of a breeding pair has an equal probability of being affected by a volcanic eruption given that albatrosses share parental duties with both parents alternating egg incubation and chick rearing shifts throughout the breeding season (Tickell, 2000).

An above-ground volcanic eruption on Torishima could result in several situations that would result in the death of birds at the colony. For example, lava flowing down the mountain has the potential to cover incubating adults and chicks. Additionally, fine ash in the air could damage a bird's respiratory system. Evidence from Laysan albatross suggests that albatross may not immediately leave their eggs or chicks during an eruption; adults continued to incubate eggs when their nests were inundated by flood waters (2007, Guadalupe Island, R.W. Henry, pers. comm.) and when attacked by rats (Kepler, 1967). We assumed that if a volcanic eruption occurred during one of the months that encompassed the eight-month breeding season, the "worst case scenario" occurred, in which eruptions caused 100% mortality of all birds present on the island (including all eggs or chicks). Additionally, we explored volcanic effects on population dynamics by (1) increasing the annual eruption probability to 10%, 20%, 30%, and 40% and (2) rendering the island inhospitable to breeding birds (i.e., setting reproductive success to zero) for 5 and 10 years following an eruption.

2.5.2. Chronic (annual) mortality

Short-tailed albatross currently experience an unknown level of chronic mortality from natural and anthropogenic sources. Some

chronic mortality sources that may potentially affect short-tailed albatross population viability are contaminants (Kunisue et al., 2006), fisheries bycatch (Anonymous, 1999), and disease (Weimerskirch, 2004). Additional chronic mortality was assigned by increasing annual mortality by 1, 2, 4, 6 and 8 percentage points over estimated current mortality levels across age classes (except for the egg to fledge stage) and we assumed that these threats have independent, non-interacting effects and that both males and females were affected equally. Even with the highest increase in annual mortality (8%), these mortality rates still fall within the ranges reported for other albatross species (Table 3). As albatross chicks usually require the survival of both adults in order to fledge (Tickell, 2000), in model scenarios that had added adult mortality, egg to fledge survivorship was adjusted (to account for the increased probability of death of a parent) using the following equation:

$$S_{c_{new}} = (S_{c_w} / (S_a^{(8/12)})^2) * (S_{a_{new}}^{(8/12)})^2$$

where $S_{c_{new}}$ and $(S_{a_{new}}^{(8/12)})^2$ are the new chick and adult survivorships (of both parents) during the eight-month breeding season with added adult mortality, respectively; S_{c_w} is the current estimated survivorship of a chick (including effects of parental mortalities); and $(S_a^{(8/12)})^2$ is the current survivorship of both parents during the eight-month breeding season without added mortality.

2.6. Elasticity analysis

2.6.1. Deterministic methods

To determine the sensitivity of the stochastic growth rate to changes in vital rates, an elasticity analysis was run for mean deterministic matrices (Caswell, 2001). For each rate, with the exception of egg to fledge survivorship (which was obtained from short-tailed albatross demography), we calculated the elasticity for matrices constructed with the lowest values for that rate, 1000 vital rate set mean, and highest value for that rate, with all other rates held at their 1000 vital rate set mean (Table 2).

2.6.2. Stochastic methods

We calculated the elasticity of the stochastic population growth rate in relationship to the probability of a volcanic eruption and additional chronic mortality for the stochastic matrix (1000 simulations and 1000 years) as per Morris and Doak (2002). We chose conditions near current estimates, with a probability of volcanic eruption of 2.2% per year and an added chronic mortality of 1% per year.

3. Results

3.1. Catastrophic volcanic eruptions

Volcanic eruptions occurring at their historic frequency (probability of eruption = 2.2% per year) on Torishima slightly, but not substantially, reduced (from 1.064 to 1.059) the mean stochastic population growth rate (1000 simulations over a 50 and 100 year time frame). Even though a volcanic eruption can reduce the population size considerably, the relatively high and constant population growth rate allowed for a rapid rebounding of the population within a few years of a catastrophic event (Fig. 2a). In fact, following a volcanic eruption that occurs in January, when breeding adult colony attendance is 50% (Appendix B), the population rebounds to its pre-eruption size in less than 10 years (mean time = 8.9 years, 1000 simulations, starting population size = 1485). Not until a volcanic eruption occurred on average 4 times every 10 years did the population growth rate become negative (Fig. 2b) and only after the probability of a volcanic eruption was increased to 30% did the probability of extinction over 100 year projections (1000

Table 3
Chronic mortality rates reported for several albatross species. Added chronic mortality rates used in short-tailed albatross models (2–8%) were within observed mortality rates for other albatross species.

Species	Mortality source	% mortality increase	Reference
Amsterdam (<i>Diomedea amsterdamensis</i>)	Bycatch	6.5	Weimerskirch et al. (1997)
Wandering (<i>D. exulans</i>)	Bycatch	5.4	Weimerskirch and Jouventin (1998)
Black-footed (<i>Phoebastria nigripes</i>)	Bycatch	4.8	Lewison and Crowder (2003)
Waved (<i>P. irrorata</i>)	Bycatch	3.3	Awkerman et al. (2006)
Yellow-nosed (<i>Thalassarche chlororhynchos</i>)	Disease (avian cholera)	~8	Weimerskirch (2004)

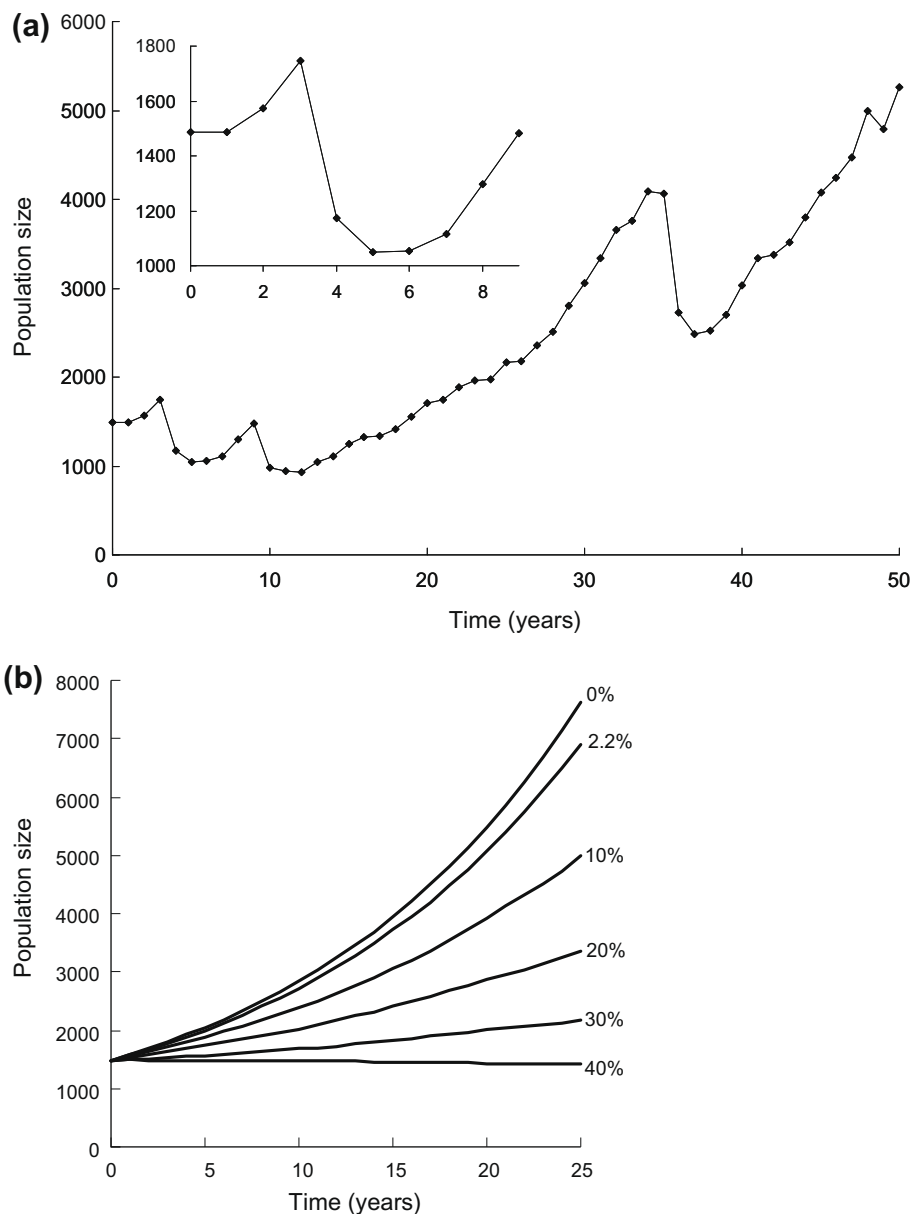


Fig. 2. (a) Projected short-tailed albatross population size over 50 years at the Torishima colony, illustrating population declines following volcanic eruptions in years 4, 10 and 36 (single model simulation). Inset shows detailed population trajectory before and after a volcanic eruption in year 4. As widowed birds begin to re-mate, the high growth rate allows the population to rapidly recover from a volcanic eruption. (b) Mean (1000 stochastic simulations) short-tailed albatross projected population size over 25 years with the annual probability of catastrophic eruption modelled from 0–40%. Short-tailed albatross population growth remained positive until the probability of a volcanic eruption equalled 40% per year, which is approximately 18 times more frequent than the observed eruption probability of 2.2%.

simulations) become greater than 5% (Fig. 3). A main factor protecting the population against a volcanic eruption is that the maximum short-tailed albatross attendance on Torishima at any given time is only 25% (Fig. 4).

Additionally, we found little effect on population dynamics if breeding was halted (i.e., reproductive success was zero) on Torishima for 5 and 10 years following a volcanic eruption. In model simulations (probability of eruption = 2.2% per year, 100 years,

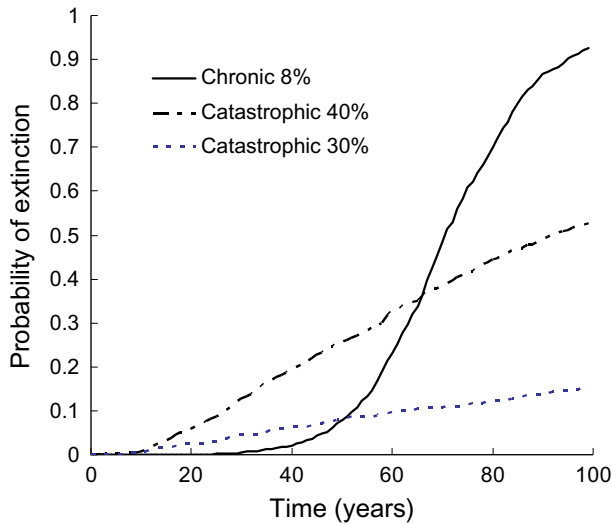


Fig. 3. Short-tailed albatross extinction probabilities for volcanic eruption frequencies of 30% and 40% per year and 8% added chronic mortality. Even though an increase in chronic (annual) mortality did not cause extinction in the short-term (up to 40 years), an added chronic mortality of 8% resulted in a high probability (>90%) that the population would ultimately become extinct over the next 100 years. Probabilities were based on 1000 simulations.

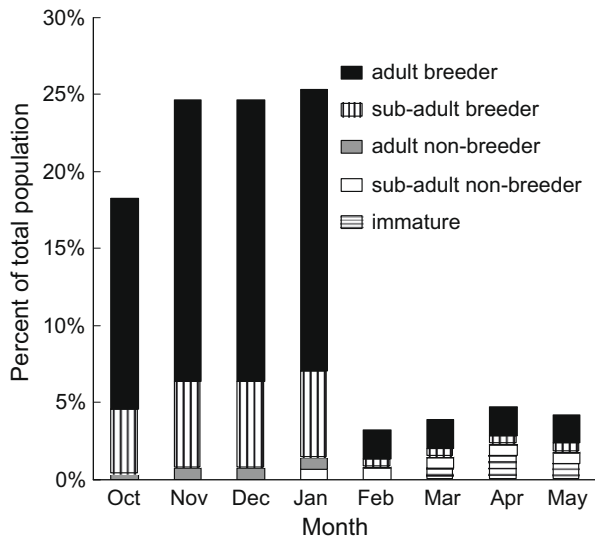


Fig. 4. Percent of the total short-tailed albatross population present on Torishima (and thus potentially killed from a volcanic eruption) per month during the breeding season (October–May), reported by stage class. The greatest percent of the population on the colony during a given month was 25%, between the months of November through January. Data adapted from Laysan albatross (Fisher and Fisher, 1969; Appendix B).

1000 simulations) with zero reproductive success for five and ten sequential years post eruption, the mean stochastic lambda was 1.05 and 1.04, respectively with none of the simulations for either scenario ever dropping below the quasi-extinction threshold.

We note that our model may underestimate the impact of a volcanic eruption because we estimated short-tailed albatross colony attendance during the breeding season (see Appendix B) from Laysan albatross data (Fisher and Fisher, 1969). In order to assess how colony attendance could influence the population-level impact of a volcanic eruption, model simulations (probability of eruption = 2.2% per year, 100 years, 1000 simulations) were conducted

with increased colony attendance. Lambda was only slightly reduced (mean stochastic lambda = 1.058 ± 0.007 SD vs. 1.059 ± 0.007 SD) when attendance values, and thus mortality during a volcanic eruption, were doubled (non-breeder and immature attendance (October–March) as well as breeder attendance during chick rearing (February–May)). Given these findings, we feel that the uncertainty surrounding our estimation of colony attendance for short-tailed albatross did not significantly affect our reported results.

3.2. Chronic mortality

Adding chronic (annual) mortality of 1% to adult, sub-adult, juvenile and fledge-to-1-year survivorships caused a 2.5-fold greater decrease in stochastic lambda than did incorporating mortality from catastrophic volcanic eruptions at the historic eruption probability of 2.2% per year. On average, the population size decreased when added chronic mortality was greater than or equal to 6% (Fig. 5). Short-tailed albatross population projections (1000 simulations over 100 years) never reached the quasi-extinction threshold with 2% or 4% added chronic mortality. However, at 8% added mortality, the population reached the quasi-extinction threshold in 92.5% of the simulations (1000 simulations over 100 years), almost twice the probability of extinction for model simulations of a population experiencing a volcanic eruption probability of 40% per year (Fig. 3).

3.3. Deterministic elasticity analysis

As predicted from other population models of long-lived species with high adult survivorship (Arnold et al., 2006; Awkerman et al., 2006; Crowder et al., 1994), elasticity analysis of vital rates used in the deterministic matrix demonstrated that short-tailed albatross adult survivorship had the greatest effect on lambda (Fig. 6a). Noteworthy was that the elasticities did not change appreciably over the range (low, mean, high) of vital rate values evaluated (Fig. 6a).

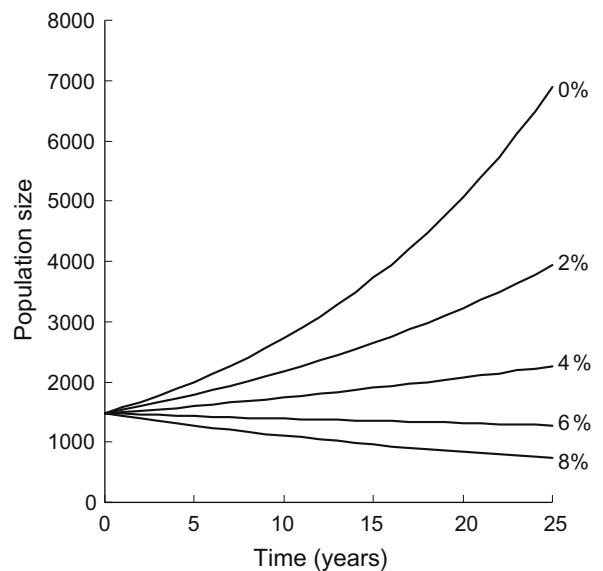


Fig. 5. Mean short-tailed albatross population size over 25 years on Torishima, averaged from 1000 stochastic simulations using different added chronic (annual) mortality rates with historical volcanic eruption frequency of 2.2% per year. An added chronic mortality of 6% per year or greater resulted in a negative population growth.

3.4. Contrasting catastrophic and chronic mortality

A stochastic elasticity analysis demonstrated that the population growth rate is three times more sensitive to changes in chronic mortality than to changes in volcanic eruption frequency (Fig. 6b). At the current probability of volcanic eruption (2.2%), the mean stochastic growth rate (1.058) for the short-tailed albatross population is achieved with an annual mortality rate of ~0.8% (Fig. 7). If mortality remains at this current rate, but the eruption frequency increases, the population will keep growing until the eruption probability exceeds 30%, a 15-fold (and unrealistic) increase. In contrast, if the eruption probability remains at its current rate but chronic mortality rates increase, the population

will continue to grow until annual mortality exceeds 5.5%, a 7-fold increase.

4. Discussion

Catastrophic events are considered devastating to population persistence, although there is a lack of published evidence on their effects. A literature search (March 2008) using the Web of Science database and the keyword “population viability analysis” generated 487 returns. Only 4% (21) of the 487 returns included analysis of catastrophic threats (identified by narrowing our search using the keyword “catastroph”) and just six of these 21 publications used empirical knowledge about the frequency and/or severity of the catastrophe. Furthermore, merely five of the 21 catastrophic publications (1% of the 487 original returns) included analysis of both catastrophic and chronic threats. We constructed a stochastic PVA with chronic and catastrophic threats and determined that, in contrast to increases in chronic low-level mortality, natural catastrophic events (volcanic eruption) had almost no detectable influence on the long-term persistence of the critically endangered short-tailed albatross.

Short-tailed albatross' pelagic nature, with ~75% of the population at-sea during any given time (Fig. 4), appears to buffer them against the catastrophic effect of a volcanic eruption, even one that kills all adult and juvenile birds present on the island. However, when birds experienced a low-level (1%) added chronic (annual) mortality, the population growth rate declined measurably (Fig. 5). The population growth rate became negative, with a declining projected population, when adult mortality levels were ~5.5%, a mortality rate well within annual mortality levels observed in other albatross species (Table 3). Our findings are supported by a recently published population model on short-tailed albatross that predicted an additional removal of 50 birds per year – equal to ~2.5% increase in annual mortality – would cause a significant impact on population growth as evidenced by a delay in reaching short-tailed albatross recovery goals (Zador et al., 2008).

Fisheries bycatch (USFWS, 2005; Zador et al., 2008) is believed to be one of the main sources of anthropogenic mortality for short-tailed albatross. Bycatch rates of seabirds are extremely difficult to estimate (Baker et al., 2007; Lewison et al., 2004a; Miller and Skalski, 2006; Uhlmann et al., 2005), yet are thought to be the main cause of the downward population trends seen in most albatross species worldwide (Arnold et al., 2006; Awkerman et al., 2006; Lewison and Crowder, 2003). Mortality rates for fisheries bycatch of black-footed albatross, a related northern hemisphere species, were estimated by Lewison and Crowder (2003) to be between 5200 and 13,800 birds per year. Assuming a global population size of 278,000 birds (IUCN, 2006), the annual bycatch rate for black-footed albatross ranges from 1.9% to 5.0%. A similar bycatch rate for short-tailed albatross would result in a far less optimistic picture of their future population viability.

Based on satellite telemetry data, short-tailed albatross primarily forage within the exclusive economic zones of the United States, Russia, and Japan, as well as in international waters (Suryan et al., 2007, 2006). As such, even though United States mitigation measures (NMFS, 2007) may have dramatically reduced fisheries bycatch of albatrosses (Dietrich et al., 2008), bycatch rates from other Pacific Rim countries with absent or less stringent mitigation and observer programs may significantly affect short-tailed albatross populations. Our findings that chronic mortality (from both natural and anthropogenic sources) is the most important threat to short-tailed albatross population persistence underscores the importance of closely monitoring short-tailed albatross cumulative bycatch rates across all pertinent fisheries, such that temporal changes in the number of birds caught are rapidly detected.

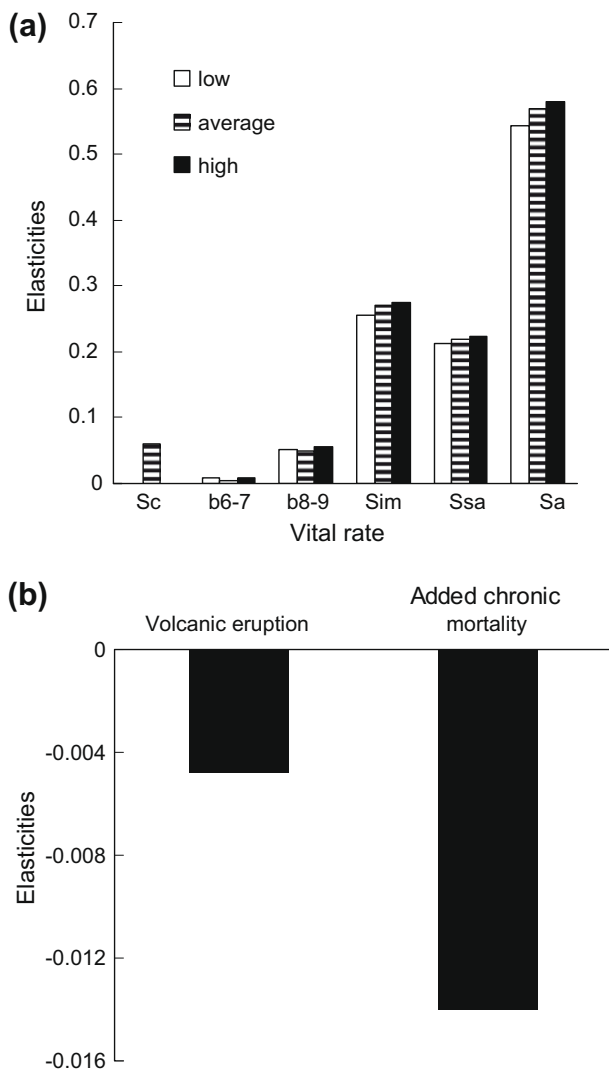


Fig. 6. (a) Elasticity values for the deterministic matrix demonstrate that adult survival (Sa) has the greatest effect on short-tailed albatross population growth. For elasticities of vital rates with more than one mean value (Table 1), we calculated the elasticity for matrices constructed with the lowest, 1000 vital rate set mean, and highest value for that rate, with all other rates held at their 1000 vital rate set mean. The 1000 vital rate set mean values for the probability of breeding for 6 and 7 year olds (b6–7), probability of breeding for 8 and older (b8–9), immature survival (fledge to 4; Sim), sub-adult survival (5–8; Ssa) and adult survival (9+; Sa) were 0.551, 0.885, 0.904, 0.958, 0.975, respectively. Egg to fledge survivorship (0.515; Sc) was obtained from short-tailed albatross demography. (b) Elasticities of short-tailed albatross stochastic population growth demonstrate that added chronic mortality (1% per year) had a much greater (~3-fold) effect on lambda than the probability of a volcanic eruption (2.2% per year). Elasticities are negative because increasing either variable (eruption frequency, chronic mortality) decreased lambda values.

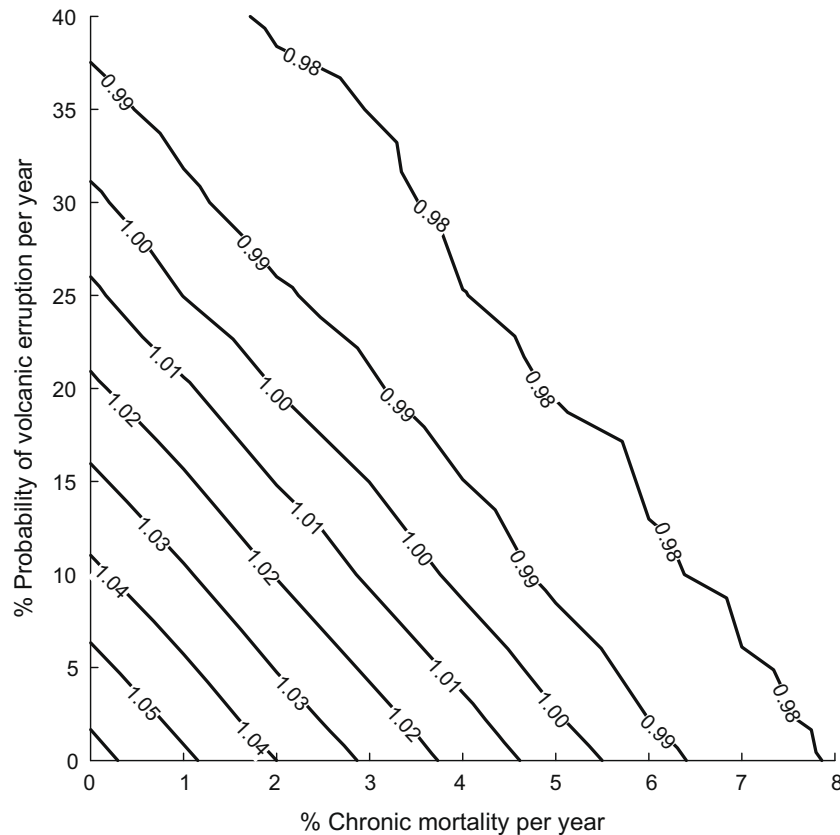


Fig. 7. Relative contribution of chronic (contaminant effects, disease, bycatch) and catastrophic (volcanic eruption) mortality on short-tailed albatross population growth (lambda, denoted by the contour lines). The mean stochastic growth rate for the short-tailed albatross population on Torishima (1.058) is achieved at a 2.2% per year probability of eruption and a chronic mortality rate of ~0.8% per year. Short-tailed albatross population size declines when the population growth rate falls below 1.00.

In addition to fisheries bycatch, exposure to marine pollutants (e.g., organochlorines, plastic) and disease may also pose chronic threats to short-tailed albatross. Persistent organic pollutants (e.g., dioxins and related compounds) have been found in short-tailed albatross at concentrations similar to black-footed albatross (Kunisue et al., 2006). Contaminant levels in black-footed albatross are of concern (Auman et al., 1997) with a recent study reporting significant associations between organochlorine compounds and altered immune function (Finkelstein et al., 2007). Consequently, short-tailed albatross population viability may also be at risk from contaminant-induced effects, especially with respect to compromised immune function. Immune function is important for disease resistance and Weimerskirch (2004) suggested that disease outbreaks may have contributed to the 5–10% increase in adult mortality observed in the yellow-nosed albatross (*Thalassarche chlororhynchos*) population on Amsterdam Island. Therefore, although as yet undocumented, contaminant-related effects that could lead to increased risk for disease transmission and infection may be or become significant sources of mortality for short-tailed albatross.

Despite a paucity of demographic data for our focal species, we were able to build stochastic models that allowed us to evaluate the relative effects of chronic and catastrophic threats on short-tailed albatross population persistence. By borrowing data from several albatross species, using short-tailed albatross census data, and incorporating uncertainty throughout our analysis, we were able to obtain clear results concerning short-tailed albatross general population dynamics and their likely response to multiple potential threats. Nonetheless, direct estimates of short-tailed albatross demographic rates from field studies are important to monitor the future population trajectory of this

species, which is especially relevant since this population is one of the only albatross species in the world that is currently showing robust growth, or even stability. In particular, we recommend that (1) annual censuses of the number of eggs laid and fledgling success be conducted for the two primary short-tailed albatross colonies: Torishima and Senkaku, and (2) mark-recapture studies be conducted at Torishima and Senkaku to estimate adult and sub-adult survivorship as well as track changes in survivorship over time.

Our results have direct relevance for the management of the highly endangered short-tailed albatross. While a great deal of concern has concentrated on the possible consequences of a volcanic eruption, less attention has focused on the possible effects from increases or decreases in chronic mortality. Our work suggests that eruptions are not likely to threaten the continued recovery of this species, and that efforts to start a new population on a non-volcanic island, motivated by this perceived risk alone, may not be needed. However, we fully support the need for (at the minimum) a second population due to the possible future occurrence of chronic threats (e.g., introduced predators, disease) on Torishima or unanticipated effects of an eruption (i.e., lava flows rendering the entire island unsuitable for nesting for the foreseeable future). Undeniably, a wide range of unforeseen circumstances could jeopardize the Torishima population, and a stable and protected second population is paramount to assure the continued survival of short-tailed albatross.

In conclusion, short-tailed albatross are buffered against the effects of localized environmental catastrophes due to their wide-ranging foraging behavior and high capacity for population growth, presumably driven by their current high adult survival rates. Consequently, while the threat of a volcanic eruption is

rear their chicks through May. There is no colony attendance from June to September.

References

- Abrams, P.A., 2002. Will small population sizes warn us of impending extinctions? *American Naturalist* 160, 293–305.
- Anonymus, 1999. Short-tailed albatross *Phoebastria albatrus* deaths in the North Pacific fishery. *Bird Conservation International* 9, 190.
- Arnold, J.M., Brault, S., Croxall, J.P., 2006. Albatross populations in peril: a population trajectory for black-browed albatrosses at South Georgia. *Ecological Applications* 16 (1), 419–432.
- Auman, H.J., Ludwig, J.P., Summer, C.L., Verbrugge, D.A., Froese, K.L., Colborn, T., Giesy, J.P., 1997. PCBs, DDE, DDT, and TCDD-EQ in two species of albatross on Sand Island, Midway Atoll, North Pacific Ocean. *Environmental Toxicology and Chemistry* 16, 498–504.
- Austin, 1949. The status of the Steller's albatross. *Pacific Science* 3, 283–294.
- Awkerman, J.A., Huyvaert, K.P., Mangel, J., Shiguetto, J.A., Anderson, D.J., 2006. Incidental and intentional catch threatens Galapagos waved albatross. *Biological Conservation* 133 (4), 483–489.
- Baker, G.B., Wise, B.S., 2005. The impact of pelagic longline fishing on the flesh-footed shearwater *Puffinus carneipes* in Eastern Australia. *Biological Conservation* 126, 306–316.
- Baker, G.B., Double, M.C., Gales, R., Tuck, G.N., Abbott, C.L., Ryan, P.G., Petersen, S.L., Robertson, C.J.R., Alderman, R., 2007. A global assessment of the impact of fisheries-related mortality on shy and white-capped albatrosses: conservation implications. *Biological Conservation* 137, 319–333.
- Breining, D.R., Brugman, M.A., Stith, B.M., 1999. Influence of habitat quality, catastrophes, and population size on extinction risk of the Florida scrub-jay. *Wildlife Society Bulletin* 27, 810–822.
- Caswell, H., 2001. *Matrix Population Models: Construction, Analysis, and Interpretation*. Sinauer, Sunderland, MA, USA.
- Coulson, T., Mace, G.M., Hudson, E., Possingham, H., 2001. The use and abuse of population viability analysis. *Trends in Ecology and Evolution* 16, 219–221.
- Crowder, L.B., Crouse, D.T., Heppell, S.S., Martin, T.H., 1994. Predicting the impact of turtle excluder devices on loggerhead sea-turtle populations. *Ecological Applications* 4, 437–445.
- Cuthbert, R., Ryan, P.G., Cooper, J., Hilton, G., 2003. Demography and population trends of the Atlantic yellow-nosed albatross. *Condor* 105 (3), 439–452.
- Dietrich, K.S., Melvin, E.F., Conquest, L., 2008. Integrated weight longlines with paired streamer lines – best practice to prevent seabird bycatch in demersal longline fisheries. *Biological Conservation* 141, 1793–1805.
- Finkelstein, M.E., Grasman, K.A., Croll, D.A., Tershy, B.R., Keitt, B.S., Jarman, W.M., Smith, D.R., 2007. Contaminant-associated alteration of immune function in black-footed albatross (*Phoebastria nigripes*), a North Pacific predator. *Environmental Toxicology and Chemistry* 26, 1896–1903.
- Fisher, H.I., 1976. Some dynamics of a breeding colony of Laysan albatrosses. *Wilson Bulletin* 88 (1), 121–142.
- Fisher, H.I., Fisher, M.L., 1969. The visits of Laysan albatrosses to the breeding colony. *Micronesica* 5 (1), 173–221.
- Gerber, L.R., Hilborn, R., 2001. Catastrophic events and recovery from low densities in populations of otariids: implications for risk of extinction. *Mammal Review* 31, 131–150.
- Gerrodette, T., Gilmartin, W.G., 1990. Demographic consequences of changed pupping and hauling sites of the Hawaiian monk seal. *Conservation Biology* 4, 423–430.
- Good, T.P., Davies, J., Burke, B.J., Ruckelshaus, M.H., 2008. Incorporating catastrophic risk assessments into setting conservation goals for threatened Pacific salmon. *Ecological Applications* 18, 246–257.
- Hanson, F.B., Tuckwell, H.C., 1981. Logistic growth with random density independent disasters. *Theoretical Population Biology* 19, 1–18.
- Hasegawa, H., DeGange, A.R., 1982. The short-tailed albatross, *Diomedea albatrus*, its status, distribution and natural history. *American Birds* (September), 806–814.
- Hughes, T., 1994. Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral-reef. *Science* 265, 1547–1551.
- Hunter, C.M., Moller, H., Fletcher, D., 2000. Parameter uncertainty and elasticity analyses of a population model: setting research priorities for shearwaters. *Ecological Modelling* 134, 299–323.
- Inchausti, P., Weimerskirch, H., 2001. Risks of decline and extinction of the endangered Amsterdam albatross and the projected impact of long-line fisheries. *Biological Conservation* 100 (3), 377–386.
- Inchausti, P., Weimerskirch, H., 2002. Dispersal and metapopulation dynamics of an oceanic seabird, the wandering albatross, and its consequences for its response to long-line fisheries. *Journal of Animal Ecology* 71, 765–770.
- IUCN, 2006. 2006 IUCN red list of threatened species. <<http://www.iucnredlist.org>>.
- Kelly, M.J., Durant, S.M., 2000. Viability of the Serengeti cheetah population. *Conservation Biology* 14, 786–797.
- Kepler, C.B., 1967. Polynesian rat predation on nesting Laysan albatrosses and other Pacific seabirds. *Auk* 84, 426–430.
- Kunisue, T., Nakanishi, S., Oka, N., Sato, F., Tsurumi, M., Tanabe, S., 2006. Dioxins and related compounds in albatrosses from the Torishima Island, Japan: accumulation features by growth stage and toxicological implications. *Environmental Science and Technology* 40, 6919–6927.
- Kuno, H., 1962. *Catalogue of the Active Volcanoes and Solfataras Fields of Japan, Taiwan and Marinas*. International Association of Volcanology, Rome.
- Lande, R., 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* 142, 911–927.
- Lewison, R.L., Crowder, L.B., 2003. Estimating fishery bycatch and effects on a vulnerable seabird population. *Ecological Applications* 13, 743–753.
- Lewison, R.L., Crowder, L.B., Read, A.J., Freeman, S.A., 2004a. Understanding impacts of fisheries bycatch on marine megafauna. *Trends in Ecology and Evolution* 19, 598–604.
- Lewison, R.L., Freeman, S.A., Crowder, L.B., 2004b. Quantifying the effects of fisheries on threatened species: the impact of pelagic longlines on loggerhead and leatherback sea turtles. *Ecology Letters* 7, 221–231.
- Ludwig, D., 1999. Is it meaningful to estimate a probability of extinction? *Ecology* 80, 298–310.
- Mangel, M., Tier, C., 1994. 4 facts every conservation biologist should know about persistence. *Ecology* 75, 607–614.
- Marmontel, M., Humphrey, S.R., Oshea, T.J., 1997. Population viability analysis of the Florida manatee (*Trichechus manatus latirostris*), 1976–1991. *Conservation Biology* 11, 467–481.
- McCarthy, M.A., 1996. Extinction dynamics of the helmeted honeyeater: effects of demography, stochasticity, inbreeding and spatial structure. *Ecological Modelling* 85, 151–163.
- Miller, T.J., Skalski, J.R., 2006. Estimation of seabird bycatch for North Pacific longline vessels using design- and model-based methods. *Canadian Journal of Fisheries and Aquatic Sciences* 63, 1878–1889.
- Morris, W.H., Doak, D.F., 2002. *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis*. Sinauer Associates, Sunderland, MA.
- Nantel, P., Gagnon, D., Nault, A., 1996. Population viability analysis of American ginseng and wild leek harvested in stochastic environments. *Conservation Biology* 10, 608–621.
- Nel, D.C., Taylor, F., Ryan, P.G., Cooper, J., 2003. Population dynamics of the wandering albatross *Diomedea exulans* at Marion Island: longline fishing and environmental influences. *African Journal of Marine Science* 25, 503–517.
- Nilsson, T., 2004. Integrating effects of hunting policy, catastrophic events, and inbreeding depression, in PVA simulation: the Scandinavian wolf population as an example. *Biological Conservation* 115, 227–239.
- NMFS (National Marine Fisheries Service), 2007. Fisheries of the exclusive economic zone off Alaska: groundfish and halibut fisheries of the Bering Sea and Aleutian Islands management area and Gulf of Alaska, seabird avoidance measures revisions. In: *Federal Register* 72 (18 December), US Government Printing Office, Washington, DC, USA, pp. 71601–71605.
- Oli, M.K., Holler, N.R., Wooten, M.C., 2001. Viability analysis of endangered Gulf Coast beach mice (*Peromyscus polionotus*) populations. *Biological Conservation* 97, 107–118.
- Rolland, V., Barbraud, C., Weimerskirch, H., 2009. Assessing the impact of fisheries, climate and disease on the dynamics of the Indian yellow-nosed albatross. *Biological Conservation* 142, 1084–1095.
- Root, K.V., 1998. Evaluating the effects of habitat quality, connectivity, and catastrophes on a threatened species. *Ecological Applications* 8, 854–865.
- Sagar, P.M., Molloy, J., Weimerskirch, H., Warham, J., 2000. Temporal and age-related changes in survival rates of Southern Buller's albatrosses (*Thalassarche bulleri bulleri*) at the snares, New Zealand, 1948 to 1997. *Auk* 117 (3), 699–708.
- Sanger, G.A., 1972. The recent pelagic status of the short-tailed albatross. *Biological Conservation* 4, 189–193.
- Suryan, R.M., Sato, F., Balogh, G.R., Hyrenbach, K.D., Sievert, P.R., Ozaki, K., 2006. Foraging destinations and marine habitat use of short-tailed albatrosses: a multi-scale approach using first-passage time analysis. *Deep-Sea Research Part II – Topical Studies in Oceanography* 53, 370–386.
- Suryan, R.M., Dietrich, K.S., Melvin, E.F., Balogh, G.R., Sato, F., Ozaki, K., 2007. Migratory routes of short-tailed albatrosses: use of exclusive economic zones of North Pacific Rim countries and spatial overlap with commercial fisheries in Alaska. *Biological Conservation* 137, 450–460.
- Tickell, W.L.N., 2000. *Albatrosses*. Yale University Press, New Haven.
- Tryjanowski, P., Sparks, T.H., Profus, P., 2009. Severe flooding causes a crash in production of white stork (*Ciconia ciconia*) chicks across Central and Eastern Europe. *Basic and Applied Ecology* 10, 387–392.
- USFWS (US Fish and Wildlife Service), 2005. Short-tailed Albatross Draft Recovery Plan. US Fish and Wildlife Service, Anchorage, AK, p. 62.
- Uhlmann, S., Fletcher, D., Moller, H., 2005. Estimating incidental takes of shearwaters in driftnet fisheries: lessons for the conservation of seabirds. *Biological Conservation* 123, 151–163.
- Weimerskirch, H., 2004. Diseases threaten Southern Ocean albatrosses. *Polar Biology* 27, 374–379.
- Weimerskirch, H., Jouventin, P., 1998. Changes in population sizes and demographic parameters of six albatross species breeding on the French sub-Antarctic Islands. In: Robertson, G., Gales, R. (Eds.), *Albatross Biology and Conservation*. Surrey Beatty and Sons Pty Limited, Chipping Norton, pp. 84–91.
- Weimerskirch, H., Brothers, N., Jouventin, P., 1997. Population dynamics of wandering albatross *Diomedea exulans* and Amsterdam albatross *D. amsterdamensis* in the Indian Ocean and their relationships with long-line fisheries: conservation implications. *Biological Conservation* 79 (2–3), 257–270.
- Weimerskirch, H., Zimmermann, L., Prince, P.A., 2001. Influence of environmental variability on breeding effort in a long-lived seabird, the yellow-nosed albatross. *Behavioral Ecology* 12 (1), 22–30.
- Whitman, K.L., Starfield, A.M., Quadling, H., Packer, C., 2007. Modeling the effects of trophy selection and environmental disturbance on a simulated population of African lions. *Conservation Biology* 21, 591–601.
- Zador, S.G., Punt, A.E., Parrish, J.K., 2008. Population impacts of endangered short-tailed albatross bycatch in the Alaskan trawl fishery. *Biological Conservation* 141, 872–882.