Evaluating population impacts of predation by owls on storm petrels in relation to proposed island mouse eradication

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Abstract.   We quantify the expected demographic benefit to a seabird of conservation concern, the ashy storm-petrel *Oceanodroma homochroa,* from the proposed eradication of introduced house mice *Mus musculus* on the South Farallon Islands, California. A key objective of the eradication is to reduce storm petrel predation by burrowing owls *Athene cunicularia,* which stopover on the island during their fall migration. Mouse trapping and field surveys of both owls and depredated storm petrel carcasses conducted during 2000–2012 reveal a strongly seasonal, inter-related pattern among the three species: When owls arrive during the fall, mice are super-abundant and the overwhelming choice of prey for those owls that remain. In the winter, the mouse population crashes just as storm petrels begin to arrive in large numbers; owls that remain on the island switch to preying upon storm petrels until May, when they depart to breed. Capture–recapture analyses of storm petrels showed (1) annual adult survival was inversely related to owl abundance, especially during January–April, and (2) storm petrels demonstrated a declining trend in abundance 2006–2012. The latter was associated with low rates of adult survival, high abundance of overwintering burrowing owls, and high incidence of depredated storm petrels. To evaluate projected impacts to storm petrels of a change in owl predation, we developed a Leslie matrix model, incorporating environmental stochasticity. We modeled future storm petrel population trajectories, allowing for different levels of owl-mediated predation. Our results suggest that a reduction in owl abundance, a projected consequence of the elimination of mice, has the potential to substantially reduce overall storm petrel mortality, thereby reducing storm petrel declines and increasing the likelihood of stable trends in the future. While long-term benefits to storm petrels of mouse eradication are apparent, the risk of increased predation due to prey-switching by owls also needs to be addressed. This study highlights uncertainty of outcomes, which must be considered in evaluating management impacts. This study demonstrates the value of concurrent, continuous, long-term datasets in providing a quantitative basis for management to aid the conservation of species of concern.

Key words: apparent competition; introduced species; island ecosystems; Leslie matrix; population dynamic models; population stochasticity; predation; rodent cycles; seabird conservation.

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INTRODUCTION

Colonially breeding seabird populations face major threats worldwide, including climate change, habitat loss, overharvesting and bycatch, invasive species, pollution, and disease (Wilcove et al. 1998). When compared with other birds, seabirds produce few young per year, begin breeding at an older age, and have higher adult survival (Weimerskirch 2002). The low intrinsic

population growth rates and the generally limited anti-predator adaptations of island-breeding species (Carey et al. 1996, Borrelle et al. 2016) underline concern about population impacts of predators on seabirds, especially in the presence of non-native species. For extremely long-lived, low-fecundity species such as those in the order Procellariiformes, which includes the storm petrels, shearwaters, and albatrosses, adult survival is the key demographic parameter in determining population growth or decline (Nur and Sydeman 1999). Management actions to counter threats to seabird survival can be difficult to implement, but elimination of introduced species impacting seabird colonies has proved successful (Russell 2011, Jones et al. 2016).

Natural resource managers are often concerned with the potentially severe effects of predators on island-breeding seabird species, where direct predation on species that evolved without land-based predators can cause significant population declines (Krajick 2005). However, indirect interactions may also have severe impacts and exacerbate predation on species of concern (Thomsen et al. 2018). One example is hyper-predation, which involves interactions among three species: a predator; a primary prey species, which may be an introduced species; and a secondary prey species, often a species of conservation concern. In hyper-predation, there is enhanced predation pressure on the secondary prey, due to an increase in the abundance of a predator population that displays a numerical response to the primary prey and/or a sudden decline in the abundance or availability of the primary prey (Courchamp et al. 2000, Howald et al. 2007). This indirect interaction among prey species has also been referred to as "apparent competition" (DeCesare et al. 2010, Holt and Bonsall 2017). A notable example of this phenomenon on an island is provided by the interaction of the predator barn owl (*Tyto alba*) in relation to its primary prey, the deer mouse (*Peromyscus maniculatus*), and its secondary prey, the seabird, Scripps's murrelet (*Synthliboramphus scrippsi*; Thomsen et al. 2018).

In this study, we analyze field data and develop statistical and population models to elucidate the inter-relationships among three species: a seabird of conservation concern (ashy storm-petrel, *Oceanodroma homochroa*; henceforth

"storm petrel"), a native predator (burrowing owl, *Athene cunicularia*; henceforth "owl"), and an invasive rodent (house mouse, *Mus musculus*; henceforth "mouse"), occurring on Southeast Farallon Island, California (SEFI; Fig. 1). We focus on characterizing the current impacts of owl predation on storm petrels, as a means to quantify the projected population-level consequences for the storm petrel of a proposed eradication of the mouse (USFWS 2019).

The ashy storm-petrel has been the subject of much study on the Farallon Islands National Wildlife Refuge (Ainley et al. 1990, Ainley 1995, Sydeman et al. 1998*a*). Due to major population declines, threats from colony predation, and a high risk of at-sea mortality (e.g., from oil spills), the species has been listed as a California Species of Special Concern (Carter et al. 2008). In addition, the ashy storm-petrel is currently listed as endangered by IUCN (BirdLife International 2018) due to its restricted geographic range, small population size, and apparent declines (Sydeman et al. 1998*a*, Ainley and Hyrenbach 2010, Carter et al. 2016). The South Farallon Islands represent the largest colony for this species, with perhaps 40–50% of the world population (Carter et al. 2016). Storm petrels exhibit marked seasonality in attendance and activity on SEFI. They are rare or absent for most of November and December but begin to attend the colony in larger numbers in late January (Ainley et al. 1990). Breeding typically occurs between May and August, with storm petrel numbers, including breeding and non-breeding individuals, peaking in June (Ainley et al. 1990; Point Blue, *unpublished data*). In August, storm petrel abundance declines rapidly as all failed breeders and non-breeding individuals depart the colony. By late October, more than 85% of chicks have fledged and any remaining adults only visit the colony briefly every few nights to feed chicks until they are old enough to fledge (Point Blue, *unpublished data*).

The western burrowing owl (*A. c. hypugaea*) breeds throughout much of California and other western states, but on the Farallones these owls are strictly overwintering migrants (no records of breeding; DeSante and Ainley 1980, Gervais et al. 2008, Poulin et al. 2011). Owls arrive on the Farallones during their southbound fall migration, usually starting in September and peaking
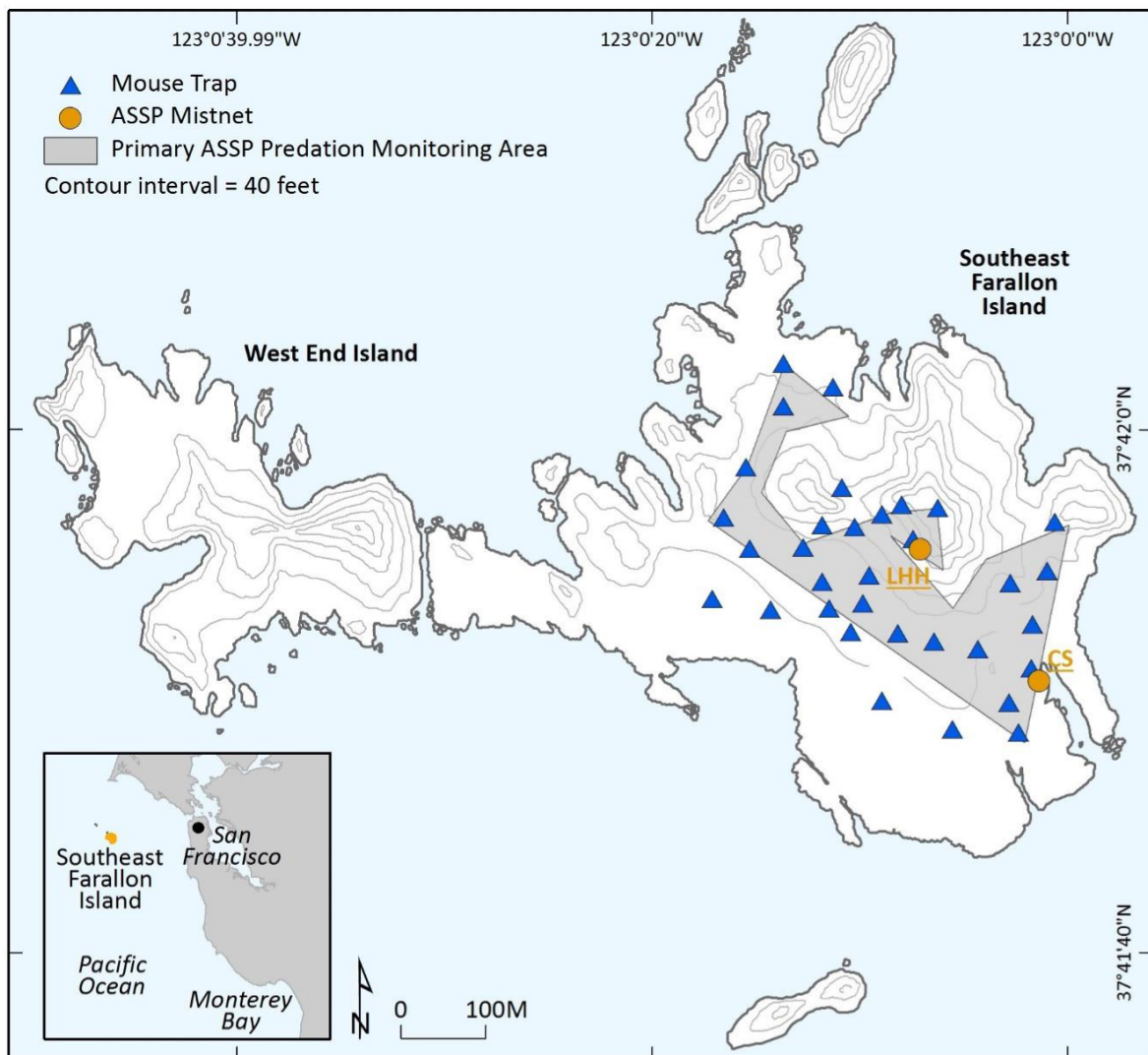
Fig. 1. Ashy storm-petrel netting sites, mouse trapping locations, and storm petrel predation survey areas on South Farallon Islands, CA; Southeast Farallon Island, and West End Island shown. ASSP is Ashy storm-petrel. Inset depicts general location of the Farallon Islands relative to San Francisco. Contour interval is 40 feet (12.19 m).

in October when the mouse population is also at its annual peak (Irwin 2006). Whereas some owls may depart fairly quickly, others remain on the islands for up to four months or more, all departing by May (DeSante and Ainley 1980; Point Blue, *unpublished data*). Burrowing owls are generally considered opportunists and feed on a variety of prey items including invertebrates and small vertebrates, with rodents dominating by biomass (Poulin et al. 2011).

House mice are one of the most widespread invasive mammals on earth (Bronson 1979, Brooke and Hilton 2002) and have been shown to have significant impacts on plant, invertebrate, and seabird communities (Howald et al. 2007, Wanless et al. 2007, 2012, Angel et al. 2009). Mice are present on SEFI year-round but abundance varies dramatically during the year, with low numbers from January to June, a sharp increase in the fall, and then rapid decline in the winter

(Irwin 2006). During their peak abundance, mouse density has been estimated at >1000 mice per ha, one of the highest reported mouse densities for any island in the world (Grout and Griffiths 2013). In contrast, island house mouse densities elsewhere commonly range from 10 to 250 per ha (MacKay et al. 2011, McClelland et al. 2018).

Though house mice on islands are known to depredate seabird eggs and chicks (Bolton et al. 2014, Dilley et al. 2015), there is little evidence of such direct effects of mice on breeding seabirds on the South Farallon Islands (Ainley and Boekelheide 1990, Point Blue, *unpublished data*). Rather, mice have an indirect impact on storm petrels through the hyper-predation of burrowing owls. On SEFI, owls subsist almost entirely on a diet of mice in fall and early winter (Chandler et al. 2016, Mills 2016). However, as the mouse population crashes in early winter, overwintering owls switch from a diet dominated by mice in December to one dominated by storm petrels in February, with the January diet displaying a mixture of the two prey species (Chandler et al. 2016). Thus, storm petrels, which are nocturnal at the colony, as are the foraging owls, become a major prey item for the owls in the late winter and spring (Chandler et al. 2016, Mills 2016).

In this study, we estimate mortality impacts of owls on storm petrels and then incorporate this information into a population dynamic model of storm petrels, based on analyses of data collected on all three species since 2000. We quantify the effect of owl predation on storm petrel survival during the period, 2000–2012, as a means to make projections regarding the future. Our long-term study of storm petrels on the Farallon Islands indicates that future population trends, with or without mouse eradication, are difficult to predict, and thus, we explicitly incorporate this uncertainty into our projections. Additionally, we discuss whether once mice are eradicated, prey switching by owls, could adversely affect the storm petrel population.

Methods

This study drew on five main datasets for the three species examined, both for analysis and development of the storm petrel population dynamic model (see Table 1). We pursued a four-phased approach. (1) We examined variation in abundance among the three species with regard to intra-annual variation and analyzed field data on intensity of predation by owls on the storm petrel during the same period. (2) Using data from a long-term capture–recapture mist-netting study of the storm petrel on SEFI (Bradley et al. 2011), we estimated change in storm petrel population size over time. (3) We analyzed the potential effect of inter-annual variation in owl abundance on storm petrel predation by first characterizing the change over time in predator abundance and an index of predation events. Then, using the capture–recapture dataset

Table 1. Summary of datasets used in this study.

Datasets	Parameter(s) addressed	Principal time scale	Time series	Notes
Mouse trapping success	Monthly variation in mouse abundance	Month	2001–2004; 2010–2012	Used all data available through 2012
Burrowing owl abundance index	Monthly and annual variation in abundance of the predator	Month	2000–2012	Standardized surveys began 2000; color banding started in 2007
Index of owl predation on storm petrels	Monthly and annual variation in predation rates as indicated by prey carcasses	Month	2003–2012	Standardized carcass surveys began 2003
Capture–recapture histories of banded storm petrels	Annual variation in population size and adult survival; also annual survival in relation to owl abundance	Annual	Capture histories: 2000–2014, used to estimate parameters for 2001–2012	Analyses use captures from 2000 on, when owl surveys began
Reproductive success of storm petrels	Mean and variance of reproductive success among breeding individuals; also reproductive success in relation to owl abundance.	Annual	2000-2012	Used annual means and SEs to estimate mean and variance in stochastic population model

analyzed in Phase 2, we analyzed annual variation in adult survival and estimated the effect of variation in the abundance of owls on the South Farallon islands on adult storm petrel survival rates. (4) We constructed a stochastic population dynamic model that accounts for the current population trend, based on our survival estimates, and incorporates data on reproductive success of the Farallon population. We then modeled the storm petrel population to estimate potential changes in its trajectory that might be expected given a hypothesized reduction in owl abundance in response to the proposed eradication of the owl's primary prey, the house mouse.

Phase 1: Variation in abundance/predation rates over time for focal species

House mouse abundance.—We created an index of mouse abundance based on trapping success along 4 transects spread across island habitats (Irwin 2006; Fig. 1). Trapping success was then summed on a monthly basis as the proportion of trap nights in which a mouse was captured; see Appendix S1 for details.

Owl abundance index.—An index of owl abundance was determined from daily surveys conducted from standardized observation locations along trails or from blinds during periods of known owl presence—usually September to May, depending on arrival and departure of first and last owls. These standardized surveys were conducted from January 2000 to December 2012 (Table 1), as described in Appendix S1. In addition, beginning in fall 2007, owls were color banded, which allowed better subsequent identification of individual owls and their roosts.

To reduce effects of variation in daily sighting effort of owls as well as variation in daily detection probability, we developed a simple but robust index of owl abundance, consisting of the maximum number of individual owls seen on any single day, calculated for each month. This index (monthly maximum value) better accounted for missed detections on individual daily surveys and displayed a higher correlation with the storm petrel predation index (see *Storm petrel predation index*) than did the monthly mean or minimum values.

Storm petrel predation index.—We developed a monthly index of predation on storm petrels from standardized carcass surveys conducted throughout the island between January 2003 and December 2012 (details in Appendix S1).

Identified remains were classified as predation by western gulls, owls, or unknown predator based on their condition (see Appendix S1 for criteria). As with the owl surveys, not all of the South Farallon Islands can be surveyed for storm petrel remains, and thus, while that likely covers a majority of storm petrel breeding habitat and areas where owl predation regularly occurs, ours is an index collected in a standardized fashion, not an absolute measure, of predation. Here, we assume that the pattern of monthly and annual owl predation rates on storm petrels in surveyed areas are representative of the entire island.

Reproductive success of storm petrels.—Reproductive success (defined as the number of chicks fledged per breeding pair) was monitored for a subsample of nest sites in rock wall habitat around the island. Beginning 4 May, nests were checked every five days using a flashlight or flexible borescope to determine their contents (adult/egg/chick, etc.) and monitoring continued for active breeding sites until the last chick fledged. Additional details of methods, which generally follow that of Ainley et al. (1990), are presented in Appendix S1. Mean and between-year variance in reproductive success for 2000–2012 were used in the stochastic population model (details in Appendix S3).

Statistical analyses in Phase 1 were carried out with STATA 15.1 (StataCorp 2017).

Phase 2: Estimating change in storm petrel populations over time

Determination of absolute population size of seabirds is difficult, especially for species such as storm petrels, whose nests are difficult to access or observe (Ainley et al. 1990, Sanz-Aguilar et al. 2010, Ismar et al. 2015). Standardized mist netting of banded individuals provides an opportunity to estimate population size and thus changes in population size over time, using capture–recapture methods.

We analyzed mist net capture histories of uniquely banded storm petrels at two sites on SEFI from 2000 to 2014 (Fig. 1). We then fit Jolly-Seber models to estimate temporal variation in population size. Detailed mist-netting methods are included in Appendix S1.

For all storm petrel survival and population modeling, we excluded presumed transients from analyses. Transient individuals are those with very low, or zero, site fidelity in contrast to those sub-adults and adults displaying high site fidelity (Pradel et al. 1997). We refer to the latter as residents. The presence of transients and residents in the same dataset violates the assumption of homogeneity of capture/recapture probability in capture–recapture models and leads to biased estimation of survival (Lebreton et al. 1992, Nur and Geupel 1993). We used a double-capture criterion to distinguish residents from presumed transients, an approach that has been validated and successfully applied to several passerine species (Nur et al. 2004, Peach and Baillie 2004). An individual could be classified as a resident if (1) the individual was captured more than once, at least 7 d apart, in the same season or (2) it was captured in more than one year. However, in the latter case, the capture history was only included in the analysis from the year of second capture. Thus, individuals that were only caught once were presumed to be transients and not included in the analysis (Nur et al. 2004).

We used the program MARK sub-module POPAN (in the R programming language; R Core Team 2018, using the library RMark; Laake et al. 2015) to estimate population size in each year (Cooch and White 2019:12), based on these capture histories. We constructed a capture history table that included all resident storm petrels captured April–August of each year, from 2000 through 2014. Note that an individual caught before 2000 was included in this analysis if it was also caught at least once between 2000 and 2014 (conforming to the double-capture criterion). See Appendix S2 for details regarding POPAN modeling methods.

We then used the year-by-year POPAN-derived estimates of population size to characterize population trajectory during the period 2002–2012. We did this by constructing a set of simple quantitative models based on the ln-transformed population estimates from the POPAN model above. The set of candidate models examined included Year as linear, quadratic, and cubic polynomial, as well as no trend (i.e., slope of zero). In addition, we considered that changes in population trend may have been abrupt rather than gradual (Bestelmeyer et al. 2011). To examine this possibility, we used linear splines, also referred to as change point analyses, fitting models with two linear segments joined at a knot (Harrell 2001:18, Ainley et al. 2013).

Each linear segment required a minimum of four years of data. We considered models with change points at all possible years meeting that requirement (i.e., 2005, 2006, 2007, 2008, and 2009) as well as change points mid-way between the specified years (2005/2006, 2006/2007, etc.), resulting in a total of 13 candidate models. The preferred model of population trajectory was then chosen by comparing AIC_c among candidate models and used as a basis for the population dynamic modeling in phase 4.

Phase 3: Analyzing indices of predation on storm petrels and the impact of owl predation on storm petrel survival

Variation over time for owl abundance and storm petrel predation indices.—We obtained best fit models for trends in the owl abundance index, from 2000 to 2012, and storm petrel predation index, for 2003–2012, using an approach similar to that used for identifying the trajectory of storm petrel population over time (Phase 2). That is, we considered a suite of models including linear, polynomial, and linear spline models. We used AIC_c to compare among candidate models and present the statistical analysis of the preferred model in relation to year for owl abundance and storm petrel predation, respectively.

Statistical estimation of survival of storm petrels, including effects of burrowing owls.—We used MARK to analyze storm petrel capture–recapture histories in order to estimate annual survival and recapture probabilities by fitting and analyzing competing Cormack-Jolly-Seber (CJS) models (Lebreton et al. 1992, Laake et al. 2015, Cooch and White 2019) using captures from 2000 through 2014. First, in order to characterize the change in survival over time, we analyzed fully time-dependent CJS models (Lebreton et al. 1992, Cooch and White 2019), similar to that described for population estimation. We considered Φ to be either fully time-dependent or constant. We modeled p as constant across years, fully time-dependent, or as a linear function of netting hours in each year. In addition, we considered models in which p either was, or was

not, a function of netting site. Thus, we compared a set of 12 models (2 alternative parameterizations for $\Phi \times 6$ alternative parameterizations for p). As with the POPAN models, we compared models with respect to AIC_c and the difference in likelihood, and also considered whether all model parameter values were estimable and standard errors could be obtained.

Secondly, we evaluated models to estimate the effects of burrowing owls, if any, on storm petrel survival. We considered models with a burrowing owl abundance effect only, models that allowed for temporal variation in survival (as above), and models that included both effects. Parameterization and criteria for choosing the preferred model were the same as used to model survival over time.

The potential effect of burrowing owls was modeled as a linear term with respect to the owl abundance index. Here, we use the average of monthly values for the period September–April, the 8 months during which owls are present on the island, which are also the 8 months leading up to and including the beginning of the storm petrel breeding season (April). We considered other monthly intervals for this index (e.g., just the months January–April) but results were similar and model fit was not improved doing so. Thus, the first year that could be analyzed was 2001 (where owl abundance was estimated for September 2000–April 2001).

Results of the mark–recapture analysis were incorporated into the predictive population dynamic model in two ways. First, the statistical model results were used to estimate the change in logit survival with a change in the annual owl abundance index (Cooch et al. 1996). The change in logit survival was then converted into a change in absolute survival which was then used in the population model (see Phase 4). Second, we determined the total among-year variation in annual survival and, following Cooch and White (2019), estimated the proportion of variance due to sampling error, with the remaining variance, termed "process variance" (Gould and Nichols 1998), included in the stochastic modeling (Appendix S3). The fraction of the total process variance due to variation in owl abundance was also estimated (Appendix S3).

We used the U-CARE module (in program MARK) to model goodness of fit (GOF), using the full-time-dependent CJS model (U-CARE cannot provide GOF tests for models with individual covariates, such as owl abundance). Results were used to estimate ĉ and adjust likelihood ratio tests accordingly (as described in Cooch and White 2019: 5).

Phase 4: Modeling storm petrel population trends: current and future population scenarios

Stochastic population modeling.—To assess and quantify the impact of a change in owl abundance and predation on Farallon storm petrel population trajectory, a presumed consequence of mouse eradication, we developed a stochastic population dynamic model for the Farallon Island storm petrel population using RAMAS GIS 5.0 (Akçakaya 2005). We developed a Leslie matrix, with an age structure corresponding to the stable age distribution associated with the Leslie matrix. The elements of the Leslie matrix were then modified in relation to presumed reduction of mortality as result of a projected reduction in the abundance of owls. We also incorporated stochastic variation in fecundity and survival; for each element of the Leslie matrix, RAMAS randomly chose a value drawn from a distribution whose mean was determined as described above and whose standard deviation (SD) reflected process variation associated with that parameter (see Appendix S3).

Starting population size.—Our analysis focused on changes in projected population trends instead of absolute population numbers. Therefore, we depict population modeling results, with and without impacts of mouse eradication, by setting relative population size in Year 0 to Year 1.0. Thus, projected population size in Years 1–20 can be readily compared to Year 0, corresponding to the breeding season immediately following successful mouse eradication. Thus, if eradication occurs in November–December of Year T, then the population model starts with a breeding population of specified size in the following April–August (i.e., Year 0, which corresponds to Year $T + 1$). We then compare simulated population trajectories under the three owl abundance scenarios: no owl reduction, moderate reduction, and large reduction.

Calibrating the Leslie matrix.—Reproductive success was based on recent observations in the field

(see above and Appendix S1). Other demographic parameter estimates are described in Appendix S3. We calculated the adult survival rate such that, with the other parameter values fixed, the matrix produced a population whose finite population growth rate corresponded to the observed trend. Survival rates of juveniles and sub-adults were scaled accordingly (Nur and Sydeman 1999).

Modeling population impacts of owl predation.—Using the calibrated stochastic population model, we projected population change 20 yr into the future. This was done assuming that baseline mean and SD for survival and fecundity values corresponding to the recent, observed trend, will continue unchanged over this period. Next, we simulated population trajectories over a 20-yr period resulting from a change in storm petrel survival, brought about by a hypothesized reduction in owl abundance, where the projected change in storm petrel survival probability was derived from our statistical analysis. We used data from the last 4 yr of the time series (2009–2012) to obtain an estimate of recent owl abundance, which is higher than in the earlier years of the time series, and then consider scenarios in which owl abundance changes in the future as a result of mouse eradication. There is considerable uncertainty as to the degree to which owl attendance (and thus owl-mediated predation) will be reduced. To capture this uncertainty, we consider two hypothetical scenarios of reduced owl attendance: mean reductions of 50% and 80%. These values refer to average long-term reductions in owl abundance in future years, on which basis we have modeled a statistically estimated change in storm petrel survival.

Furthermore, we assumed that first-year and second-year storm petrel survival did not improve as a result of owl reduction; only the survival of third-year and older individuals improved. While age of first breeding is confirmed at age 4, there are little data regarding the presence of second- and third-year individuals on the Farallon Islands. For the purposes of modeling, we therefore assumed that second-year birds are absent from the island, but that third-year birds are present (e.g., may be prospecting for breeding opportunities) and are as susceptible to predation as are older individuals (see Sydeman et al. 1998*a*).

Here, we only model a change in survival due to a reduction in owl predation; we had an insufficient basis to model changes in fecundity resulting from reduced owl abundance (see Appendix S3).

Incorporation of uncertainty into the analyses.—We incorporated uncertainty into the modeling results by (1) considering the impacts of two different levels of owl reduction and (2) incorporating stochasticity of demographic parameters, for both fecundity and survival, in our population modeling. In addition, we developed two alternative population dynamic models in which the baseline population trend (in the absence of a change in owl abundance) was greater by 2.25% or 4.5% per yr than was the observed baseline trend. However, we found that the change in population trend due to a projected change in the magnitude of owl predation was insensitive to the magnitude of the baseline trend. Hence, we only present modeling results that use the recent, observed trend as the baseline (pre-owl reduction) trend for storm petrels.

Results

Phase 1: Variation in abundance/predation rates over time for focal species

Monthly variation for the three focal species.—House mouse abundance, owl abundance, and storm petrel predation by owls each showed a clear and distinctive seasonal pattern (Fig. 2). For mice, the population index was lowest in February–May and highest in August–December (Fig. 2; Appendix S4). For owls, the abundance index was high in October–March and near zero in June–August (Fig. 2), when owls are absent from SEFI and adults are breeding on the mainland (Gervais et al. 2008). The index of owl predation on storm petrels was highest in February–April, and near zero in June–December (Fig. 2). Thus, two temporal trends are of note: (1) The storm petrel predation index increases from January to February, peaking in March, just as the mouse index drops precipitously, and (2) at the time that burrowing owls arrive on the island (in September and October), mouse populations are at peak levels (Fig. 2). Despite the presence of both owls and storm petrels in September and October (Ainley et al. 1990), predation on storm petrels appears to be near zero at this time (Fig. 2).
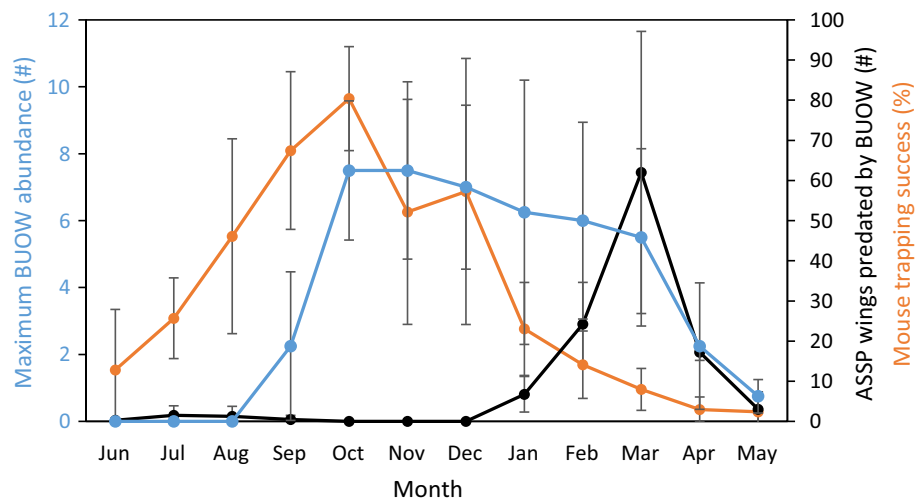
Fig. 2. Monthly variation in three key metrics: mouse abundance index (2001–2004, 2011–2012; orange), index of storm petrel predation by burrowing owls (2008–2012; black), and burrowing owl abundance index (2008–2012; in blue) at Southeast Farallon Island. Mean monthly values and standard deviations are shown.

Most of the monthly variation in the storm petrel predation index (ln-transformed) was explained by variation in owl abundance and the mouse abundance index ($n = 29$; $R^2 = 0.538$; R^2adj = 0.502; $P < 0.0001$). After controlling for mouse abundance, owl predation on storm petrels was significantly related to owl abundance ($\beta = +0.199 \pm 0.056$, $P = 0.001$). Likewise, the storm petrel predation index was significantly negatively correlated with mouse abundance, after controlling for owl abundance ($\beta = -3.46 \pm 0.67$, $P < 0.001$).

Patterns of annual variation in the predation index and owl abundance index are presented in Phase 3.

Phase 2: Estimating change in storm petrel populations over time

Storm petrel population size, as determined by POPAN, varied strongly between 2002 and 2012 (Fig. 3). The two best models for characterizing population trajectory, with regard to AIC$_c$ and estimability of parameters, were change point models. Both models had similar AIC$_c$ values (difference of 0.18 units): Either a change point in 2005 or mid-way between 2005 and 2006 (i.e., 2005.5) was supported. We chose a change point of 2005.5 rather than 2005 because (1) this allowed more data (4 full years) to be used to
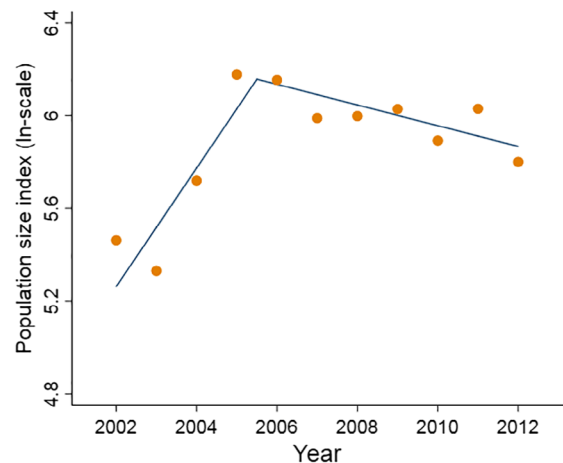

Fig. 3. Population index, by year, from POPAN Jolly-Seber model for Southeast Farallon Island ashy storm-petrels. The index is ln-transformation of population size, as estimated for the two netting sites from captures in 2000–2014. Estimates for 2002–2012 are depicted; POPAN is not able to estimate population size in 2000, 2001, or 2014 (see text). Also depicted is preferred trend-over-time model, a linear spline with change point at 2005/2006; see Table 2.

estimate the slope before the change point, with 7 yr post-change point, and (2) the population estimates for 2005 and 2006 were very similar,

Table 2. Parameter estimates from analysis of population change over time for ashy storm-petrels on Southeast Farallon Islands based on POPAN modeling.

Variables	Coefficient	SE	t	P
Year: to 2005.5	+0.2552†	0.0436	5.85	<0.001
Year: from 2005.5	−0.0446†	0.0229	−1.95	0.087

Notes: Preferred model for change over time is linear spline model with change point mid-way between 2005 and 2006 (see text, Fig. 3). Based on analysis of individual year estimates from preferred POPAN model (where Φ, time-dependent; p, site + hours + time-dependent; pent, time-dependent; N, site). Dependent variable is ln(population size), from POPAN estimates, weighted by the inverse of the standard error (SE) of the estimate. Number of observations = 11. $F_{(2,8)} = 18.82$; $P < 0.001$. $R^2 = 0.825$; $R^2 \text{adj} = 0.781$, $\text{AIC}_c = -9.277$.

† Test of differences in coefficients. Up to 2005.5 vs. since 2005.5: $F_{(1,8)} = 24.96$; $P = 0.001$.

consistent with the assumption that the change in trend occurred between the two years (a difference of 2.3%, $P > 0.5$; Fig. 3). Note that the difference in slope before and after the change point was significant ($P = 0.001$) whether the change point was 2005 or 2005.5. Reproductive success for SEFI storm petrels was similar between the earlier and later periods (mean = 0.56 [standard error, SE = 0.028], for 2000–2006; mean = 0.58 [0.023], for 2007–2012; Point Blue, *unpublished data*), suggesting that the recent declining population trend is not a result of a decline in productivity.

For the preferred model, the trend up to the change point was strongly increasing (29.1% per yr, SE = 5.6%, $P < 0.001$; Table 2, Fig. 3), followed by a decreasing trend from 2005.5 (4.36% per yr, SE = 2.24%, $P = 0.087$), the two slopes differing significantly (Table 2).

Phase 3: Analyzing indices of predation on storm petrels and the impact of owl predation on storm petrel survival

Annual trends in owl abundance and storm petrel predation.—Owl abundance appeared relatively stable from 2001 to 2006 and then began to increase after 2006 (Fig. 4A). The overall trend depicted is significant ($P < 0.001$; Appendix S5: Table S1A); the best fit was a 2-part spline, with a knot at 2006/2007 (Fig. 4A). The four years in the time series of highest owl abundance were the four most recent years (2009–2012). The increasing trend observed since 2006/2007 is significant
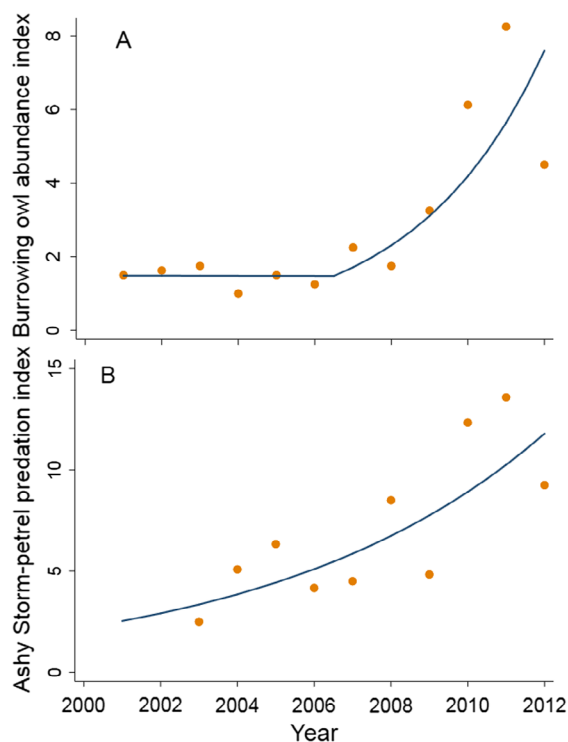

Fig. 4. (A) Variation in the annual burrowing owl abundance index for 2001 to 2012 on Southeast Farallon Island. Mean for September 2000–April 2001 is shown as 2001, etc. The abundance index was ln-transformed for analysis; the curve of best fit as determined by AIC_c, a two-part spline, is shown, back-transformed. Constant proportional change depicted for two periods: from 2001 to 2006/2007 and from 2006/2007 to 2012, with a knot between 2006 and 2007 (Appendix S5: Table S1A). (B) Annual index of burrowing owl predation on storm petrels from 2003 through 2012 on Southeast Farallon Island (monthly mean for January–December in each year).The predation index was ln-transformed for analysis; shown is the back-transformed best fit (as determined by AIC_c), a constant proportional increase from 2003 to 2012 (Appendix S5: Table S1B).

($P < 0.001$; Appendix S5: Table S1A), and this change in trend was significant ($P = 0.023$).

The index of owl predation on storm petrels significantly increased during the same period ($P = 0.006$; Appendix S5: Table S1B). The best fit of the ln-transformed predation index was a linear fit, corresponding to a constant proportional increase from 2003 to 2012 of 15.0% per yr
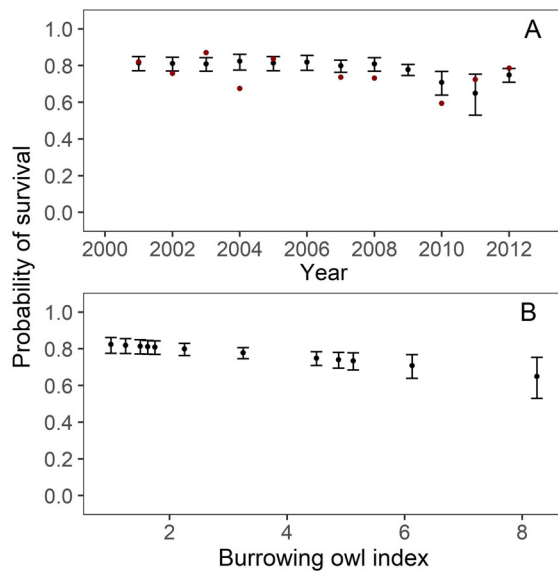
Fig. 5. Annual survival estimates for ashy storm-petrels on Southeast Farallon Island, California. Survival to the listed year is depicted (e.g., 2002 refers to survival from 2001 to 2002). (A) Survival estimates by year from the model for burrowing owl abundance (Table 3) shown in black, with 95% CIs. The fully time-dependent survival estimates (see also Appendix S5: Fig. S1) are depicted in red. (B) Adult survival as predicted by burrowing owl abundance model, for survival, as estimated for 2000/2001 to 2011/2012 (Table 3), shown in relation to the owl abundance index for that year.

(SE = 5.4%; Appendix S5: Table S1B). Thus, over the 9-yr span, the trend has been a 250% increase in the predation index (Fig. 4B). We note that the annual storm petrel owl predation index was highly correlated with the annual index of owl abundance ($R^2 = 0.740$; R^2adj = 0.703; $P = 0.003$). This result strongly suggests that the recent increase in owl abundance has indeed led to an increase in predation on storm petrels.

Analysis of storm petrel survival: goodness of fit.— We used program U-CARE to assess goodness of fit of the global CJS survival models (Choquet et al. 2009). Goodness of fit was indicated for tests 3G.Sm and M.LTEC but not for M.ITEC, indicating significant trap dependence. Results from tests 3G.Sm, M.ITEC, and M.LTEC, when summed, yielded χ^2 statistic = 97.96, df = 59 ($P = 0.001$). This provided an estimate of heterogeneity,

Table 3. Parameter estimates from ashy storm-petrel survival analysis using MARK.

Parameters	Estimate	SE	Lower 95% CI	Upper 95% CI
p: Netting hours	0.047	0.026	−0.004	0.099
Φ: Owl abundance	−0.127	0.050	−0.224	−0.030

Notes: Analysis for Southeast Farallon Island capture histories, 2000–2014. Parameter estimates for top survival model (AIC$_c$ preferred). Model, Φ as a function of linear owl abundance index; p a function of year (as factor) + netting hours. Results of likelihood ratio tests for owl abundance† and year-specific values for p‡ are included at the foot of the table; LRS and *P* values are adjusted for goodness of fit (ĉ = 1.66). AIC$_c$ = 2591.08, 2 × log likelihood = −2556.64. SE, standard error; CI, confidence interval.

† Likelihood Ratio Test (LRT) for effect of owl abundance on Φ, LRS = 3.31, df = 1, *P* = 0.069.

‡ LRT for effect of full-time dependence on p, compared to constant p, LRS = 33.04, df = 13, *P* = 0.002.

ĉ = 1.66. While not excessively large, this indicated capture heterogeneity; we adjusted likelihood ratio (LR) tests using this value.

Variation in storm petrel survival probability.— Survival estimates showed considerable variation among years (Fig. 5A) but, overall, differences among years were not significant (Likelihood Ratio Statistic (LRS) = 14.44, df = 10, *P* = 0.15, after adjusting for capture heterogeneity). Though the magnitude of variation among years was appreciable (estimates varied from 63% to 87%), standard errors for individual years were great (Appendix S5: Fig. S1). There was a tendency for survival to be higher in the earlier years compared to the more recent years, but there are also exceptions.

Our analysis of storm petrel survival in relation to owl abundance indicated that the best supported model included an effect of burrowing owl abundance, as well as an effect of year (as factor) and netting hours on capture probability (Table 3). A linear effect of owl abundance was preferred over no effect or a quadratic effect (see estimates; Fig. 5B).

Model results indicate that an increase in the owl index by 1 unit (equal to 1 individual detected, on average, per month, over the 8-month period) decreased logit storm petrel survival by 0.127 (95% confidence interval [CI]: −0.224 to −0.030; Fig. 5B). Hence, we can infer that a 50% reduction in the owl abundance index increases logit survival by 0.314; an 80% reduction in the index is expected to increase logit survival by 0.502.

Table 4. Predicted impact of a change in burrowing owl abundance on South Farallon Islands on ashy storm-petrel survival and projected population growth rate.

Change in owl abundance index	Adult survival	Change in survival	Median lambda	5th percentile lambda	95th percentile lambda
0% (no change)	0.861	0	0.952	0.908	0.988
50% decrease	0.898	0.037	0.985	0.945	1.017
80% decrease	0.916	0.055	1.001	0.963	1.031

Notes: The effect of a change in the owl abundance index of 0%, 50%, and 80% reduction is modeled, where the percent reduction is relative to mean owl abundance in 2009–2012. Adult survival, the change in survival as a result of reduction in owl abundance, and resulting finite population growth rates (lambda), as determined from median, 5th, and 95th percentile simulation results at year 20 are shown.

Phase 4: Modeling storm petrel population trends: current and future population scenarios

Population dynamic model.—We calibrated the population dynamic model to produce, on average, the observed recent decline of 4.36% per yr (Table 2, Fig. 3); adult survival in the model was 0.861 (other parameter values summarized in Appendix S3: Table S1). We then modified survival of all individuals three years and older under the two burrowing owl-reduction scenarios, that is, 50% and 80% reduction.

Storm petrel adult survival is predicted to increase by 3.7% and 5.5% for 50% and 80% owl reduction, respectively (Table 4). As a result, lambda (calculated as the median annual growth rate over the 20 yr of the simulation) increased from 0.952, with no owl reduction, to 0.985 and 1.001, respectively, for 50% and 80% owl reduction. Thus, the moderately strong observed decline is, on average, reduced in magnitude (with 50% owl reduction) or eliminated (with 80% owl reduction).

Results displayed a strong projected effect of owl reduction on median storm petrel population size even after just 10 yr (Fig. 6A). We see a change from an expected 38% decline after 10 yr, on average, with no owl reduction, to a 13% decline with 50% owl reduction, and an expected 2% increase with 80% reduction (Fig. 6A). After 20 yr, an expected decline of 63% with no owl reduction is reduced to 26% with 50% owl reduction, while the median outcome with 80% owl reduction is a 2% increase.

At the same time, a large range of outcomes can be expected under each scenario. Model results demonstrate striking variability of population trajectory across the three owl-reduction scenarios (Table 4). With 50% owl reduction, the
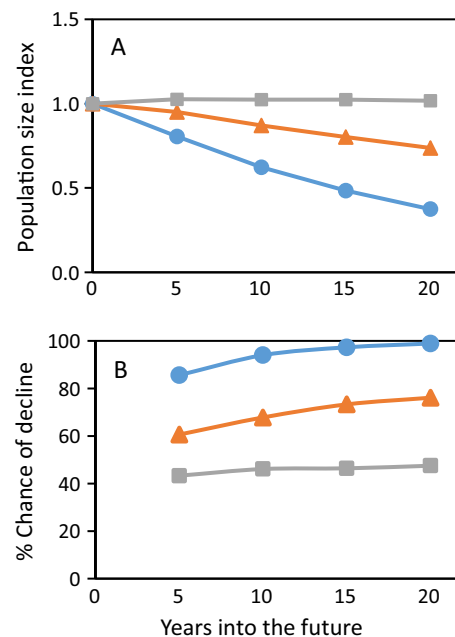

Fig. 6. (A) Farallon ashy storm-petrel population projections under the three levels of reduction in burrowing owl abundance: 0% (blue circles), 50% (orange triangles), and 80% reduction (gray squares). Median results are shown (10,000 simulations each). Depicted are relative population sizes for a 20-yr period; the population size index has been set to 1.0 for Year 0. Year 0 corresponds to the first breeding season following burrowing owl reduction. (B) Probability of population decline for the Farallon ashy storm-petrel population under three levels of reduction in burrowing owl abundance: 0% (blue circles), 50% (orange triangles), and 80% (gray squares). Depicted is the probability of a net decline, shown as percent, at the end of 5, 10, 15, and 20 yr.

median expected decline is 26%, but there is a 5% probability that the decline will be 68% or greater while there is a 5% probability of an increase of

39% or more after 20 yr (Table 4). Detailed predictions of the stochastic model are illustrated in Appendix S6, for 10- and 20-yr outcomes (Appendix S6: Figs. S1A, S1B, respectively).

The stochastic nature of the expected outcomes is also well-illustrated by considering the probability of population decline after 5, 10, 15, and 20 yr (Fig. 6B). With no owl reduction, there is a 99% probability that the population will, after 20 yr, have declined to some degree (i.e., only 1% probability of stability or growth); however, with 50% and 80% owl reduction, the probability of decline is reduced to 76% and 48%, respectively. Thus, what was an almost assured population decline is now, with 80% owl reduction, a scenario in which population stability or increase is slightly more likely than population decline.

DISCUSSION

Demographic impacts of burrowing owl predation on ashy storm-petrels

The results presented here indicate that burrowing owls have, at present, a substantial impact on ashy storm-petrel survival as revealed by the capture–recapture analyses. Results of the statistical model imply that, all else being equal, reducing owl abundance (and thus, predation) by 100% would decrease overall annual mortality from the current 13.9% to 7.9%. This calculation assumes that owl-related mortality is entirely additive, that is, that a reduction in mortality due to predation results in a concomitant increase in storm petrel survival.

While many caveats apply to any quantitative estimate, the exercise does suggest the magnitude of owl predation. Completely eliminating burrowing owl predation may not be feasible, but the population model developed here indicates that an 80% reduction in mortality due to owl predation can change a population trend for ashy storm-petrels of 4.8% decline per yr (approximate magnitude of that observed 2005/2006 to 2012) into one that is nearly stable. Even a 50% decrease in owl predation has substantial benefits over a 10- to 20-yr period. The benefit is especially marked when considering that the South Farallon Islands are home to nearly half of the world's ashy storm-petrel population (Carter et al. 2016).

The estimated mortality due to owls is large as indicated by the survival analysis, and the number of carcasses counted each year, with nearly all the mortality during the months of January–April (Fig. 2). Yet this mortality is attributed to a relatively small number of overwintering owls; the maximum number of distinct owls observed in a day has never exceeded 11 owls and is generally 6 or fewer.

The time series presented here indicate, at least through 2012, increasing trends in owl abundance and owl predation on storm petrels, coupled with a declining trend in storm petrel population, reflecting increased predation-related mortality rates. There are no published studies to indicate that the regional population of burrowing owls has increased during the time period studied. In fact, regional declines in owl populations were observed along the central and southern California coast in the years prior to and during this study (Wilkerson and Siegel 2010). Instead, evidence indicates that the change in the owl abundance index reflects a change in the duration of time that owls stay on SEFI. Detailed observations on SEFI have been made on uniquely banded burrowing owls since September 2007, identifying date of first sighting and last sighting of each banded owl in each season (September–May). From 2007/2008 to 2011/2012, the mean length of stopover per owl (ln-transformed) per year was highly correlated with the annual owl abundance index ($r = +0.965$, $P < 0.01$). This suggests that the increase in the average number of owls observed on SEFI from 2006/2007 to 2012, and increased number of predation events recorded, can be attributed to the increased length of time that owls are remaining on the South Farallon Islands. Concordantly, duration of stopover increased significantly from 2007/2008 to 2011/12 ($P = 0.002$, $n = 58$ owl stopovers).

Prey switching by burrowing owls: implications for storm petrels

Currently, predation on storm petrels is almost entirely confined to three months: February, March, and April. Since owls arrive on the island only in September–November (Point Blue, *unpublished data*), during their fall migration, what enables them to remain until late January when storm petrels first begin to return in larger

numbers, in advance of their breeding season? The answer is the extremely abundant house mouse population. As shown by Chandler et al. (2016) and here, owls appear to prefer house mice as prey, but turn to depredating storm petrels when mouse abundance has dropped severely. This prey-switching behavior has been observed to adversely impact seabirds as well as mammalian prey on islands (Roemer et al. 2002, Russell 2011, Thomsen et al. 2018) and reflects, more generally, the phenomenon of indirect or apparent competition (Wittmer et al. 2013, Serrouya et al. 2015, Holt and Bonsall 2017). On the Farallones, mice and storm petrels compete indirectly because they share a common predator. Many examples of increased predation on secondary prey due to apparent competition have been documented (Roemer et al. 2002, Courchamp et al. 2003, Serrouya et al. 2015). On Santa Barbara Island, for example, barn owls respond to a population crash of deer mice (due to El Niño conditions), by increasing predation on Scripps's murrelet (Thomsen et al. 2018). Pine marten *Martes martes* predation on Tengmalm's owl *Aegolius funereus* nests decreased in years when *Apodemus* field mouse populations increased (Zárybnická et al. 2015). In these examples, changes in abundance of one prey across years affect predation on a second prey. In contrast, on the Farallon Islands, we see prey switching occurring within a few months.

Could prey switching by owls on the Farallones lead to increased predation on storm petrels following mouse eradication, at least in the short term? This is a legitimate concern. We acknowledge that this represents an important uncertainty regarding the proposed mouse eradication. However, we maintain that, in this case, there are two lines of argument pointing to reduced, not increased, predation on storm petrels as a result of mouse eradication.

First, we note that the proposed mouse eradication protocols for the Farallones include the trapping and relocation of owls during and following eradication to reduce the risk of non-target mortality (USFWS 2019). Effective removal of owls will reduce or eliminate owl predation on storm petrels during the fall and winter period coinciding with mouse eradication, thus preventing prey switching in the year of eradication (cf. Courchamp et al. 2003).

Second, in future years, with no mice on the South Farallon Islands, we expect owl predation on storm petrels will be reduced compared to the present, not increased. Our argument hinges on the timing of arrival of burrowing owls during the fall, and the presence and availability of storm petrels during fall and early winter. Burrowing owls arrive almost entirely in September–November; median arrival date is 16 October (n = 182). Following mouse eradication, owls arriving in those months would have no abundant or reliable prey of any kind as most storm petrels have departed by October, and by the end of October, only some late breeders remain (Point Blue, *unpublished data*). From mid-November until late-December, storm petrels are rare or entirely absent and only begin to return to the South Farallon Islands in significant numbers in late January (Ainley et al. 1990).

In the absence of mice, it is not energetically feasible that burrowing owls would be able to sustain themselves during the period between late October and late January, especially from mid-November on. There are no abundant insect prey on the South Farallon islands, which accords with Chandler et al.'s (2016) finding that, overall, insects formed less than 1% of the diet biomass of burrowing owls. Nor are there reptile or amphibian prey available to owls. In short, in the absence of mice, prolonged stopover on the Farallon Islands is neither attractive nor feasible for burrowing owls. Nevertheless, short-term stopovers during fall migration may result in some predation of storm petrels. More information is needed regarding behavior and energetic requirements of burrowing owls during migration, as well as availability of storm petrels as prey during the fall, as opposed to the winter and spring.

Caveats

We acknowledge that color banding of owls starting in 2007 has facilitated the tracking of individual birds. Nevertheless, our results demonstrate a strongly increasing trend in owl abundance since September 2007, when color banding began. The estimated trend from 2007/2008 until 2012 is very similar to that obtained from the change point analysis for the period 2006/2007 to 2012 (β = 0.282 vs. 0.298). The predation index (from storm petrel carcass surveys)

demonstrated a significant increase from 2003 to 2012; moreover, owl abundance and the predation index were highly correlated ($r = +0.860$, $P = 0.001$), supporting a causal relationship between owl abundance and storm petrel survival rates.

Storm petrel survival is undoubtedly influenced by many factors, not just burrowing owls. Variability in oceanographic conditions may help explain the inter-annual pattern of survival (Bestelmeyer et al. 2011), though we found that the Southern Oscillation Index was not significantly correlated with storm petrel survival. Predation by gulls is an important mortality risk for storm petrels (Sydeman et al. 1998*b*), but western gull population size does not correlate with annual or decadal variation in storm petrel survival rates for this time period (N. Nur, *unpublished data*).

We did not consider direct impacts of house mice or burrowing owls on storm petrel reproductive success (see Wanless et al. 2012) but focused instead on impacts on storm petrel survival. Reproductive success of storm petrels may increase as a result of mouse eradication, either directly or indirectly. The direct effect would be a possible reduction in egg and chick mortality due to mouse eradication—though current and past evidence of direct mice impacts on breeding Farallon storm petrels is minimal (Ainley et al. 1990). Indirect effects would result from decreases in storm petrel parental mortality before or during the egg stage, resulting in increased breeding attempts and/or increased breeding success, as evidenced in other petrel species (Bradley et al. 1990, Hodges and Nagata 2001). Thus, mouse eradication may have even stronger beneficial effects on storm petrels than we have modeled.

Incorporation of uncertainty and the significance of stochasticity

Ours is a modeling exercise and thus characterized by several sources of uncertainty. The first uncertainty concerns the degree of reduction in owl attendance, and thus predation, that results from the proposed mouse eradication. Here, we have modeled two scenarios, ranging from an average of 50–80% reduction of owls, thus capturing some of the uncertainty in the owl response to mouse eradication, but further studies into how burrowing owl stopover

behavior may change as a result of mouse removal are warranted.

The second uncertainty concerns stochasticity of demographic parameters. Long-term studies of seabird demography, especially in the dynamic California Current, confirm the strong signal of annual- and decadal-scale variation, due to fluctuations in oceanographic condition, but also due to stochastic variation (Lee et al. 2007). Indeed, we found evidence of substantial variation in survival due to process variation: Our estimate of between-year SD due to process variation was 0.115.

The result of the stochasticity in demographic parameters is that, under the owl-reduction scenarios, survival will on average be improved, but not so in every year. Thus, population trend can show a diversity of results, even under the same owl-reduction scenario. While we may expect population decline, there may be net growth after 20 yr; the converse is true as well.

We acknowledge that there are other sources of uncertainty as well, including uncertainty regarding baseline adult storm petrel survival values prior to owl reduction. Our results reveal that the magnitude of the change in population trend is not very sensitive to assumptions of baseline survival, though it does reflect assumptions regarding the expected degree of owl reduction. We note that our estimate of 0.861 for baseline survival with current levels of owl predation and 0.898–0.916 survival under assumptions of owl reduction are consistent with survival estimates for the European storm-petrel (*Hydrobates pelagicus*; Sanz-Aguilar et al. 2010, Zabala et al. 2011) and Leach's storm-petrel (*Oceanodroma leucorhoa*; Huntington et al. 1996), which range from 0.89 to 0.94.

Implications of mouse eradication for ashy storm-petrels

In summary, there is strong evidence for current, significant impacts of owl predation on storm petrel population dynamics. To what extent mouse eradication results in reduction of owl predation on storm petrels remains to be seen, but results from this study, and eradications on other islands, indicate the potential positive and significant population response by storm petrels and other native species to the removal of invasive rodents (see review in Jones

et al. 2016). Data collected post-eradication will be especially valuable in assessing the assumptions and predictions of the modeling presented here and allow for additional modeling of owl response to mouse eradication.

While it is reasonable to expect that owl predation on storm petrels can be substantially reduced in the long term with mouse eradication, we cannot assume eradication will result in 100% reduction in owl predation. In fact, in the absence of their primary prey, in the years following mouse eradication, predation on storm petrels during September and October, when owls first arrive on the island during migration, may increase compared to the present. The payoff to mouse eradication, we postulate, is reduction in the current high levels of predation in the late winter and spring months, when storm petrels are found in large numbers and are susceptible to owl predation, as well as benefits to other native species that comprise the South Farallon Islands ecosystem.

ACKNOWLEDGMENTS

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2878/full

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Appendix S1. Study Species and Detailed Field Methods

Study Species

House mice (*Mus musculus*) were likely introduced to the South Farallon Islands around the same time that humans began exploiting the islands in the late the 1800's or early 1900's (Ainley and Lewis 1974). While documentation of house mice presence prior to the 1960's is not available, they presumably occurred well before then (Carter et al. 2016). Closed capture modeling from a mark-recapture study in 2012 estimated a density of 1,297 ± 224 mice per ha (95% CI: 799-1,792) on SEFI during the fall season, one of the highest reported mouse densities for any island in the world (Grout and Griffiths 2013). For the purpose of this study, we created an index of mouse abundance based on monthly trapping success on 4 transect lines spread across island habitats (Irwin 2006, Figure 1). Trapping was conducted for each of 3 nights per month between March 2001 and March 2004, and again from December 2010 to March 2012. Both sampling periods used the same transects, each with 7 traps per transect. For the 2010-2012 effort, 5 additional traps were added; these incorporated more of the vertical aspect of the island topography. Trapping efforts used D-Con® Ultra Set® covered snap traps baited with peanut butter and oats. Trapping success was determined as the proportion of trap-nights set per monthly session (either 84 [2001-2004] or 99 [2010-2012]) in which house mice were captured.

The ashy storm-petrel (*Oceanodroma homochroa)* is a colonially breeding species endemic to the California Current, between western Baja California, Mexico, and northern

California (Spear & Ainley 2007), with breeding populations concentrated at the South Farallon and Channel Islands (Carter et al. 2008, Carter et al. 2016). The South Farallon Islands represent the largest colony for this species, with perhaps 40-50% of the world population (Carter et al. 2016). This breeding population was estimated to be 2,660 in 1992 (Sydeman et al. 1998b), with a total population size (including adults, subadults, juveniles and non-breeders) estimated at fewer than 5,000 individuals (Nur et al. 1999). The breeding population on SEFI declined an estimated 44% from 1972 to 1992, based on population estimates for those 2 years (95% CI: 22-66% decline; Sydeman et al. 1998b). Reasons for the decline during that period may be related to oceanographic conditions and/or increases in western gulls (*Larus occidentalis*), another important predator, in storm petrel nesting areas (Figure 1; Sydeman et al. 1998a). Sydeman et al (1998a) surmised that burrowing owl predation on Farallon ashy storm-petrels was low relative to gull predation, but acknowledged a lack of data during late winter and early spring when both owls and storm petrels are present.

The western burrowing owl (*Athene cunicularia hypugaea*) has shown steady declines throughout the northern region of its range, and its range has contracted (Macias-Duarte and Conway 2015). This subspecies is listed as Endangered in Canada and is a Species of Special Concern in six states, including California (Poulin et al. 2011). In both California and more northern states, burrowing owls breed in March-August, and migrate mainly during September-October and March-May (Gervais et al. 2008, Poulin et al. 2011). The owls that migrate to the Farallones likely originate from intermountain regions farther north (Holroyd et al. 2010). Most migrating landbirds that arrive on the Farallones depart within a few days (DeSante and Ainley 1980, Richardson et al. 2003). However, owls are enticed to remain on the island for longer periods due to the abundance of mice as prey.

Indices of Storm Petrel Predation and Owl Abundance

To assess predation impacts, we developed a predation index based on systematic standardized

surveys. For each month, we counted the total number of depredated storm petrel remains based

on repeated, surveys conducted every 5 days from March to August in accessible areas of habitat

suitable for storm petrels. These samples were supplemented by collections throughout the year

obtained while accessing areas visited as part of several long term studies, conducted at

approximately the same time across all years. Though predation survey effort in the period

September to February was not as high as in March to August, effort was relatively consistent

from one year to the next. Depredated storm petrel remains were classified as predation by

western gulls, owls, or unknown predator based on their condition. Storm petrels depredated by

western gulls are ingested whole, with the regurgitated wings congealed in digestive juices. This

is in contrast to storm petrels consumed by owls, where wings are removed from the body before

consumption and left unadulterated (Bradley et al. 2011). Only remains positively identified as

being caused by owls were used in this analysis (Bradley et al. 2011). Overall examination of the

entire predation survey time series reveals equal proportion of identified owl and gull predation

(46% each) with 8% of samples classified as unknown (Point Blue unpublished data).

As part of daily monitoring operations, biologists searched SEFI for all non-breeding

terrestrial birds, including owls, and tallied the total for each species, for each day (DeSante and

Ainley 1980, Pyle and Henderson 1991, Richardson et al. 2003). While effort varied during the

course of the year (i.e., ~8 hours/day in the fall compared with ~3 hours/day in the winter; owls

are absent or rare May-August), owl survey effort was more consistent across years. We used

these daily surveys to construct an owl abundance index equivalent to the monthly maximum

count observed for each month. For the months of September to April, the index usually varied from 1 to 10 (mean = 2.85, SD = 2.78). During the four months from May to August each year, the monthly index was 0 (in 90.4% of the cases, n = 47) or 1 (the other 9.6%, n = 5). We emphasize that the SEFI surveys only cover accessible areas, that is, areas in which human presence would not cause undue disturbance to nesting seabirds, pinnipeds, or habitat, and where surveys would not present a risk for human safety. About 40% of the South Farallon Islands (including West End Island) are not regularly surveyed. Our objective is only to characterize monthly and annual variation in owl abundance, not to estimate absolute owl abundance. We have no reason to believe that temporal variation in owls in accessible areas differs from that in inaccessible areas.

Mist Netting Methods

Mist netting was conducted for 3 hours each netting session (from 22:30 – 01:30), with one or more sessions per month, as part of an on-going capture mark-recapture study (Sydeman et al. 1998a). Two mist net sites were used (Lighthouse Hill [LHH] and Carpentry Shop [CS]; Figure 1), which differ in characteristics such as exposure, proximity to primary breeding habitat, proximity to the shoreline, and bird density. Nets were only opened if there was less than 10 knots of wind and little or no moon visible, as strong winds and moonlight reduce the ability of nets to capture birds and make it easier for birds to avoid the net (Sydeman et al. 1998a). The goal was to conduct one session at each site once per month from April to August, weather permitting. Net location and net type were kept constant at these two sites for the duration of the study, using one 12 m long, 4 shelf nylon mist net (Avinet Inc.) with 30 mm mesh and a height of 2.6 m. Birds were banded with incoloy or stainless steel metal leg bands (size 1b) with unique

numbers assigned by the US Geological Survey's Bird Banding Laboratory. LHH site is south-facing, approximately half-way up Lighthouse Hill (~50 m elevation), and surrounded by extensive storm petrel breeding habitat and known high density of breeding sites (Sydeman et al. 1998a, Point Blue, unpublished). CS site is east-facing, adjacent to the ocean (~6 m elevation), in an area of less storm petrel breeding habitat, apparently fewer breeding birds, and with lower capture rates than LHH (Sydeman et al. 1998a). We restricted our analyses to the period between April 1st and August 15th, as this time period had relatively standardized effort across the entire time series 2000-2012, as well as matching periods of regular storm petrel colony attendance (Ainley et al. 1990). Egg-laying by ashy storm-petrels typically commences in May (Ainley et al. 1990).

Social attraction, in the form of broadcast recordings of ashy storm-petrel calls, was used during all net sessions to increase the chance of ashy storm-petrel captures at the netting sites. A portable cassette tape player (2000-2007) or digital music player and speaker (2008-2012) was placed at the base of the middle of the mist net and broadcast at a volume of ~65db throughout the netting sessions. The main calls on the tape were "flight calls," but in the background low frequency burrow "purring calls" and "rasping calls" are also present (Ainley 1995). The flight call rate was approximately 0.44 calls per second.

Methods for Determining Storm Petrel Reproductive Success

On the Farallones, storm petrels breed primarily in rock wall habitat and a few natural crevices in scree fields or catacombs. Beginning 4 May in each year, we checked all previously occupied breeding sites every 5 days to determine nest contents. All occupied sites were monitored for reproductive success, with a goal of at 50-60 sites monitored each season. Sites that had not been

occupied for at least 5 consecutive years were dropped from further study. We used a flashlight and, starting in 2007, a small video inspection camera ("See Snake®" RIGID Tools) to thoroughly examine each site. The camera allowed for increased sample size from 2007-2012, doubling the number of active sites we could follow. Once an egg was found or an adult was observed in incubation posture for two consecutive checks, the site was left undisturbed for 40 days before returning to check for hatch. Once a hatched chick was confirmed, the site was left undisturbed for an additional 40 days. After the second "skip" period, we resumed checking the site every five days until the chick fledged. The two "skip" periods helped reduce potential disturbance to incubating adults and young chicks. Chicks that were fully feathered and disappeared from their nesting crevice after 60 days of age were assumed to have fledged (Ainley et al. 1990). We assume similar reproductive success in accessible and inaccessible habitats. Clutch size is 1; storm petrels can relay after failed breeding attempts; such relays were also monitored (Ainley 1995). Reproductive success was determined with respect to all attempts of a pair (including relays).

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Appendix S2. Estimation of population size with POPAN.

The POPAN model of population size estimates survival probability (Φ), capture probability (p), and the probability of an individual entering the population (*pent*), in each year, as well as a single value of N, termed the "super-population" (consisting of all animals that would ever enter the population during the respective time series; Cooch and White 2019, chapter 12). With Φ, p, *pent*, and N directly estimated, population size in year t (N_t) can then be derived (Cooch and White 2019). The POPAN Jolly-Seber model includes constraints to resolve confounded parameters where these are assumed to be fully time-dependent. As a result, population size in the first and second capture years as well as the final capture year are not estimable (Cooch and White 2019). In addition, parameter estimates for individual years may not be adequately estimated in fully time-dependent models. By analyzing capture histories from 2000-2014, we were able, therefore, to obtain estimates of population size with POPAN for the years 2002-2012.

We examined 24 alternative models where Φ and *pent* were each either fully time-varying or time-constant, and p was either fully time-varying, varying with net hours, or time-constant. In addition, we considered models in which p varied with netting site, since differences in habitat between the sites may affect capture probability (Sydeman et al. 1998a). Thus, we

compared 24 models (= 2 x 2 x 3 x 2). Because our goal with the POPAN model was to determine variation in population size over time, we focused on the fully time-dependent parametrizations described above. Parameter estimates from the preferred model (with regard to Φ, p, *pent*, and N) were used to estimate population size in each year using the RMark function "popan.derived" (Laake et al. 2015).

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Appendix S3. Population Dynamic Model: Construction and Assumptions

The population dynamic model developed here incorporates six key demographic parameters (Nur & Sydeman 1999); we discuss each in turn, considering both estimation of mean values as well as annual variability, where appropriate. Mean parameter values used in the Leslie matrix are listed in Table S1; see text for explanation of parameter variances used.

i)   **Survival of adults.** Nur et al. (1999) determined that a stable population of ashy storm-petrels would require an adult survival rate of 89.2%, given other assumptions of demographic parameters, based on data then available. We did not use this survival value, but instead adjusted survival values of adults and immatures, given other parameter values used, to yield a Leslie matrix whose dominant eigenvalue matched the population trend that has recently been observed (a decline of 4.34% per year, see "Results").

    Annual variability in adult survival was estimated by first fitting a fully time-dependent CJS model in MARK, and estimating the total among-year variance in survival. We then partitioned the total variance into that due to sampling error ("sampling variance") and that due to "biological process" variance, following the method outlined by Gould & Nichols (1998) and described in Cooch & White (Appendix D; 2019). Using program RAMAS (Akçakaya 2005), survival rates in each year of the simulation were sampled

from a distribution whose SD was derived from the estimated among-year SD of the biological process variation.

Furthermore, we partitioned the between-year process variance into that due to variation in burrowing owls and that not due to owls. To estimate the fraction of the total process variance due to annual variation in owl abundance, we compared "deviance explained" for a fully time-dependent model for Φ to "deviance explained" by a model with Φ a linear function of the owl abundance index. The ratio of the two "deviances explained," was used to estimate the proportion of total process variance that was due to owls. Reduction in owl abundance was assumed to reduce between-year variance due to owls proportionately. Thus, a 50% reduction in owl abundance, for example, was assumed to reduce between-year variance specifically due to owls by that amount, but leave the other component of process variance unchanged.

ii)   **Survival of juveniles and subadults.** We followed Nur et al. (1999) and Ainley et al. (2001), and estimated survival of first-year, second-year, and third-year individuals as a fixed percentage of adult survival. The percentages used by Nur et al. (1999) were: 72%, 86%, and 98% of the adult value. The adult survival value, in turn, depended on the presumed effects of owl reduction. By the fourth year of life, ashy storm-petrels have begun breeding, and so we assumed that survival in their fourth year reached adult levels.

To estimate annual variation in juvenile and subadult survival, which was then incorporated into the stochastic model, we scaled the process variation SD for them relative to that obtained for adults (see above), given that survival (Φ) is a binomially distributed random variable and its variance is proportional to $\Phi \times (1-\Phi)$ (Mood et al. 1974). That is, the closer survival probability is to 0.50, the greater is its variance. Thus,

we assumed that between-year variation in survival differed between adults and immature

individuals only due to the binomial nature of Φ. The same adjustment in between-year

SD was made when adult and immature survival was increased due to burrowing owl

reduction.

iii) **Reproductive Success** is the number of young reared to fledging per breeding pair per

year. It is conditional on a pair actually breeding. Field methods for determining annual

reproductive success are described in Appendix S1. For the population modeling, we

used the mean reproductive success observed for this population over the period 2000-

2012. For annual variation in reproductive success, we estimated process variation, just

as described for survival (see above), following the approach of Cooch & White

(Appendix D, 2019), and from that derived the appropriate SD. We had no information to

indicate that reproductive success among those that bred varied with age, and so assumed

age-constancy. Reproductive success was assumed to be the same, irrespective of owl

reduction.

iv) **Probability of Breeding among Experienced Breeders.**   Ainley et al. (1990) reported

that, over a 12 year period on SEFI, an egg was laid in 92% of crevices that were

occupied by ashy storm-petrels. We follow Nur et al. (1999) and use this value,

assuming that all individuals who have bred before return to the colony, provided that

they have survived. Thus, among those that returned, 92% were assumed to breed. We

believe this assumption is reasonable as there are no available data to suggest otherwise.

v) **Probability of Breeding for the First Time.** No field data are available to estimate this

parameter for this species (Ainley 1995). Here we followed Nur et al. (1999) who drew

on a field study of the closely related Leach's storm-petrel (*O. leucorhoa*, Huntington et al. 1996). Nur et al. (1999) assumed that, for the Farallon ashy storm-petrel population, 10% of four-year olds, 50% of five-year olds, 90% of six-year olds, and 100% of seven-year olds were capable of breeding. In other words, by age 7, storm petrel breeding probability reached 100% of the adult value for breeding, 92% (see above). Thus, we assume that most storm petrels first bred at ages 5 or 6, but a few earlier (age 4) or later (age 7 or later).

vi)   **Balance between Emigration and Immigration.** The closest significant breeding population relative to the Farallon Islands is on the Channel Islands, at least 420 km away (Carter et al. 2008). There have been only a few records of banded birds from the Channel Islands being recaptured on the Farallones and vice versa (Nur et al. 1999, HSU unpublished, Point Blue, unpublished). From 1992 to 1997, less than 1% of all recaptured individuals on SEFI were known to have been first banded on the Channel Islands. These individuals might be dispersing widely during the subadult, pre-breeding period, as has been observed with vagrant storm petrel species detected on SEFI (Tristram's storm-petrel *O. tristrami*, Warzybok et al. 2009; fork-tailed storm-petrel *O. furcata* and wedge-rumped storm-petrel *O. tethys*, Point Blue, unpublished), but then return to their natal colonies when they reach maturity (Nur & Sydeman 1999).

Wide-ranging behavior of immature storm petrels of many species has been well documented elsewhere as well (Mainwood 1976, Love 1978, Furness and Baillie 1981, Fowler et al. 1982). Nur et al. (1999) estimated that the actual dispersal rate from the Channel Islands to the Farallones was 1.6%, a relatively low rate of immigration. In the population dynamic model we allow for some immigration and emigration (i.e., the

population is not closed) but assume that immigration equals emigration; that is, we

assume that dispersal is balanced. The empirical evidence indicates that emigration from

the Farallones to the Channel Islands is also very low, an inference supported by genetic

studies (Girman et al. 1999). If dispersal is not balanced, then population dynamic results

presented here would be affected.

Additional Modeling Assumptions

We assumed no maximum longevity. Storm petrels from SEFI show a maximum observed

longevity of 35 years (Bradley and Warzybok 2003). North American Leach's storm-petrels

have been observed to live at least to age 36 years (Huntington et al. 1996). Though we assumed

no maximum life span, we also assumed that older adults (well beyond prime breeding age, i.e.,

16 and older) displayed 5% lower adult survival rates, consistent with other studies of seabirds,

including those in the order Procellariformes (Weimerskirch 1992, Pyle et al. 1997, Nur et

al.1999). Model results were robust to the assumption of no maximum age because few adults

are expected to survive beyond age 16; the effect of assuming 5% reduction in adult survival for

old adults was to reduce population growth rate by 0.5% compared to no reduction.

We assumed no density dependence. Population density for this species is low, especially

when compared to other seabirds on the Farallones. In any case, there is no evidence of density

dependent reproductive success or survival for any storm petrel species.

We did not differentiate between males and females in the population model. The

species is monogamous, and so reproductive success of one sex equals that of the other sex. No

sex-specific information is available regarding survival or age of first breeding for this species.

In the modeling, we only consider a change in survival due to a reduction in owl

predation. It is possible that changes in owl abundance, and thus predation on storm petrels, may

also affect fecundity parameters. For example, because of loss of a mate during the period prior to egg-laying, a storm petrel is not able to breed in the spring or, if it finds a replacement mate, has reduced success (Bradley et al. 1990). However, we did not have information on mate loss; furthermore, analysis of annual reproductive success did not reveal a correlation between the owl abundance index for that year and reproductive success (unpublished). We cannot rule out an effect of owl predation on fecundity of storm petrels, but we had insufficient basis to model its impact.

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Table S1. Ashy storm-petrel demographic parameter values used to model projected population change with no owl reduction. See above for adjustments due to owl reduction.

Age	Survival Relative to Adult[†]	Annual Survival [‡]	Breeding Probability[§]	Reproductive Success [¶]
1	0.72	0.620	0	0
2	0.86	0.740	0	0
3	0.98	0.844	0	0
4	1	0.861	0.092	0.610
5	1	0.861	0.460	0.610
6	1	0.861	0.828	0.610
7-15	1	0.861	0.920	0.610
16+	0.95	0.818	0.920	0.610

[†] - Nur et al. 1999

[‡] – Survival rates calibrated to produce observed trend; see text.

[§] - Fraction of individuals breeding by age class, whether for the first time or as experienced breeders.

[¶] – Mean value, SEFI, 2000-2012.

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Appendix S4. Mouse Trapping Data

Table S1. Mouse trapping success data. Results by month and year from Southeast Farallon Island, 2001-2004; 2010-2012.

Month/ Year	Successful trap-nights	Total Trap Nights	Proportion success
Mar-01	13	84	0.155
Apr-01	3	84	0.036
May-01	6	84	0.071
Jun-01	17	77	0.221
Jul-01	24	80	0.300
Aug-01	29	82	0.354
Sep-01	64	90	0.711
Oct-01	61	77	0.792
Nov-01	70	84	0.833
Dec-01	114	168	0.679
Jan-02	42	196	0.214
Feb-02	9	182	0.049
Mar-02	9	168	0.054
Apr-02	0	168	0.000
May-02	0	84	0.000
Jun-02	0	84	0.000
Jul-02	9	84	0.107

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Aug-02	22	84	0.262
Sep-02	112	168	0.667
Oct-02	117	160	0.731
Nov-02	21	84	0.250
Dec-02	113	168	0.673
Jan-03	39	140	0.279
Feb-03	22	140	0.157
Mar-03	16	224	0.071
Apr-03	2	168	0.012
May-03	0	84	0.000
Jun-03	0	84	0.000
Jul-03	25	84	0.298
Aug-03	35	84	0.417
Sep-03	70	166	0.422
Oct-03	59	84	0.702
Nov-03	113	166	0.681
Jan-04	29	84	0.345
Feb-04	8	84	0.095
Mar-04	9	84	0.107
Dec-10	84	99	0.848
Jan-11	36	132	0.273
Feb-11	27	99	0.273
Mar-11	9	99	0.091
Apr-11	7	99	0.071
Jun-11	28	96	0.292
Jul-11	31	96	0.323
Aug-11	78	96	0.813
Sep-11	89	99	0.899

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Oct-11	98	99	0.990
Nov-11	32	99	0.323
Dec-11	9	99	0.091
Jan-12	4	99	0.040
Feb-12	13	99	0.131
Mar-12	0	99	0.000

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Appendix S5. Additional Statistical Results

Table S1. Trends of owl abundance and predation on storm petrels among years.

A. Preferred statistical model for owl abundance index (ln-transformed) in relation to year, as identified by AICc, 2001 to 2012. Number of observations = 12. $F(2,9) = 18.92$; $P < 0.001$. $R^2 = 0.808$; R^2adj = 0.765, AICc = 12.420.
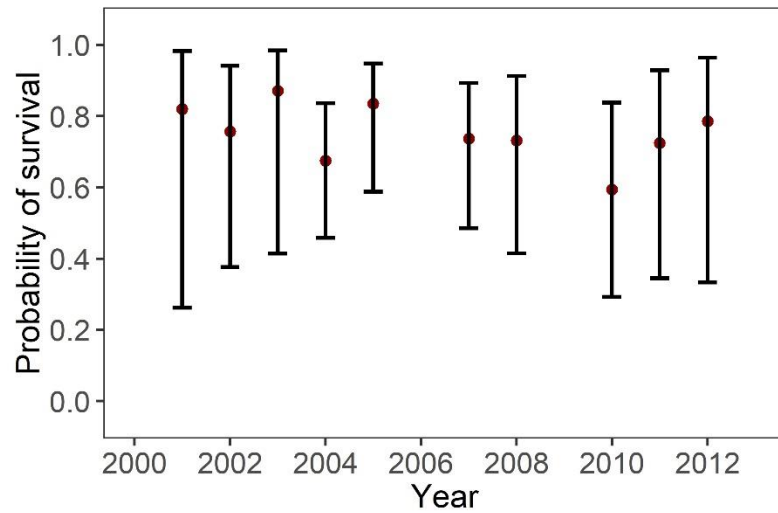
Variable	Coefficient	S.E.	P value
Year: to 2006/2007	$-0.001^{\dagger}$	0.061	$P > 0.9$
Year: from 2006/2007	$0.298^{\dagger}$	0.061	$P < 0.001$

† Test of differences in year-trend coefficients: Prior to 2006/2007 vs Since 2006/2007: $F(1,9) = 7.53$; $P = 0.023$.

B. Preferred statistical model for owl predation index (ln-transformed) in relation to year, as identified by AICc, 2003 to 2012. Number of observations = 10. $F(1,8) = 14.01$; $P = 0.006$. $R^2 = 0.637$; R^2adj = 0.591, AICc = 10.241.

Variable	Coefficient	S.E.	P value	Lower 95% CI	Upper 95% CI
Year	0.140	0.037	$P = 0.006$	0.054	0.226

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Figure S1. Annual survival estimates for ashy storm-petrels on SEFI. Survival to the listed year

is depicted (e.g., "2002" refers to survival from 2001 to 2002). Estimates from the fully time-

dependent model with 95% CIs. Program MARK could provide no estimates for 2005/2006 and

2008/2009 for this model.

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<center>**Appendix S6. Stochastic Simulation Results**</center>

Figure S1. Farallon ashy storm-petrel simulation results illustrating stochastic variation in outcomes for the owl reduction scenario: 0%, 50%, and 80% (10,000 simulations for each). 5th and 95th percentile outcome (blue triangles), 25th and 75th percentile (orange X), median (gray circle). A) Results after 10 years. B) Results after 20 years.