

1 RUNNING HEAD: Impacts of owl predation on storm petrels

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3 **Evaluating Population Impacts of Predation by Owls on Storm Petrels in Relation to**
4 **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*. One of the objectives of eradication is to reduce current levels of predation by burrowing owls *Athene cunicularia* on storm petrels on the South Farallon Islands, California. From field surveys of owls, mice, and owl depredated storm petrel carcasses conducted during 2000-2012, we found owl predation on storm petrels to be positively related to burrowing owl abundance and negatively related to house mouse abundance. During the fall, mice are the primary prey of owls, but when mouse populations crash during the winter, owls switch to preying upon storm petrels. Capture-recapture analyses of storm petrels caught during the breeding season revealed a strong increasing trend in population size to 2005/6, with a significant change in trend from increasing to decreasing for the period 2005/6-2012. The declining trend in abundance was associated with low rates of adult survival, high abundance of over-wintering burrowing owls, and high incidence of depredated storm petrels compared to before 2005. For the period 2000 to 2012, the preferred model for storm petrel annual survival included a linear negative effect of burrowing owl abundance.

To evaluate projected impacts to petrels of a change in owl predation, we considered three future “baseline trend scenarios” for Farallon storm petrels, ranging from strong decline to near-stability. We developed Leslie matrix models for each, incorporating environmental stochasticity. We used these scenarios to model a range of 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 have a substantial effect in reducing overall storm petrel mortality, thereby reducing declines and increasing the likelihood of stable or increasing trends in the future. The results also

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34 demonstrate uncertainty of outcomes, which must be considered in evaluating management
35 impacts. This study highlights the value of continuous, long-term datasets in providing the
36 quantitative basis for management to aid the conservation of species of concern.

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

INTRODUCTION

Exotic invasive species can have devastating impacts on island ecosystems (Towns et al. 2011, Russell 2011). Yet despite the considerable attention invasive species receive, and the widespread assumption that their impacts are usually negative (Martinez-Abrain and Oro 2013), there have been relatively few quantitative analyses of demographic impacts to populations of conservation concern (Parker et al. 1999). In a review of avian studies, Côté and Sutherland (1997) found that predator removal increased hatching success and population size outside the breeding season, but not necessarily breeding population size. In an extensive review on the impacts of introduced predators on seabird colonies on islands, Towns et al. (2011) detailed predator impacts on mortality and reproduction in the short term, but did not document long-term population-level impacts. There remains a pressing need to quantify the demographic impacts of predators on populations of high conservation concern (DeCesare et al. 2010).

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 an additional (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 & 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 (reviewed in Russell 2011).

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 (Schoener and Spiller 1996, Krajick 2005). However, indirect interactions may also have severe impacts and exacerbate predation on species of concern. 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, either due to an increase in the abundance of a predator population that displays a numerical response to the primary prey, or due to 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 predation” (DeCesare et al. 2010).

In this study, we analyze field data and develop statistical and population models to elucidate the inter-relationships among three species: an invasive rodent (house mouse, *Mus musculus*; henceforth “mouse”), a native predator (burrowing owl, *Athene cunicularia*; henceforth “owl”), and a seabird of conservation concern (ashy storm-petrel, *Oceanodroma homochroa*; henceforth “storm petrel”; Sydeman et al. 1998a; Carter et al. 2008), occurring on Southeast Farallon Island, California (SEFI), the largest of the South Farallon Islands (Figure 1). While there is potential for burrowing owls to impact Farallon populations of Leach’s storm-petrel (*Oceanodroma leucorhoa*) as well, they were not examined in this study due to limited Farallon demographic data on this less abundant species.

House mice are one of the most widespread invasive mammals on earth (Bronson 1979; Brooke and Hilton 2002). In island ecosystems, house mice have been shown to have significant impacts on plant, invertebrate, and seabird communities (Angel et al. 2009). Despite this, there has been less conservation action devoted to house mice on islands, relative to other introduced mammals, likely due to additional challenges in eradicating them (Wanless et al. 2007; Howald et al. 2007, Wanless et al. 2012). Though the exact timing of the introduction of house mice to the South Farallon Islands is unknown, it has been suggested to have occurred during the 1800's or early 1900's (Ainley and Lewis 1974). While late 19th and early 20th century quantitative data on mouse presence are lacking, a large population of mice has existed from the 1960s to the present, suggesting a long undocumented presence prior to the 1960s (Carter et al. 2016). Closed capture modeling from a mark-recapture study completed in one area of SEFI provided a density estimate of $1,297 \pm 224$ mice per ha (95% CI: 799-1,792), 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 50 per ha (Mackay et al. 2011).

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 direct effects of mice on breeding seabirds on the South Farallon Islands. Despite over 40 years of continuous, intensive study of breeding seabirds, few depredated eggs or chicks have been detected (Ainley and Boekelheide 1990, Point Blue unpublished). While predation on eggs by mice is difficult to detect in a crevice-nesting species, these field observations suggest the current frequency of egg predation in this population is low (Ainley and Boekelheide 1990).

The ashy storm-petrel is a seabird species of conservation concern, and has been the subject of much study on the Farallon Islands National Wildlife Refuge (Ainley et al. 1990,

Ainley 1995, Sydeman et al. 1998a). This colonially breeding species is 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). Historically, the Farallon population bred primarily in crevices on talus rock slopes, though after the creation of large rock walls and trails during the mid to late 19th century much of the breeding population appears to be utilizing the latter habitat (Carter et al. 2008; Figure 1) 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. 1999a). 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, such as Lighthouse Hill (Figure 1; Spear et al. 1987, Sydeman et al. 1998a). Sydeman et al (1998a) conjectured that burrowing owl predation on Farallon ashy storm petrels was much less than gull predation, but acknowledged a lack of data during late winter and early spring when both owls and storm petrels are present.

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 (2017) due to its restricted geographic range, small population size, and apparent declines (Sydeman et al. 1998a, Ainley and Hyrenbach 2010, Carter et al. 2016).

The burrowing owl is found throughout California and other western states (Gervais et al. 2008). Owls arrive on the Farallones starting in September, peaking in October, during their southbound fall migration (DeSante and Ainley 1980; Point Blue, unpublished). In both California and more northern states, burrowing owls breed in March-August, and migrate mainly during September-October and March-May (Haug et al. 1993, Gervais et al. 2008). Most migrating landbirds that arrive on the Farallones depart within a few days (DeSante and Ainley 1980, Richardson et al. 2003). However, owl arrivals in fall occur at the time the mouse population is at its annual peak (Irwin 2006; this study; Figure 2). Whereas some owls may depart fairly quickly, others individuals remain on the islands for up to four months or more, subsisting, in the winter, almost entirely on a diet of mice (Chandler et al. 2016; Mills 2016; Point Blue, unpublished).

During the winter months, the Farallon mouse population declines rapidly (Irwin 2006, this study; Figure 2), severely reducing their availability as prey items for owls. Consequently, burrowing owls switch to alternative prey sources over winter (Mills 2016; Chandler et al. 2016). Chandler et al. (2016) illustrated how overwintering owls switched from a diet dominated by mice in December to one dominated by storm petrels in February, with January displaying a mixture of the two prey species. Adult storm petrels, while present on the island at low levels in late fall and early winter, increase in number on the islands starting in mid-winter (Ainley et al. 1990; Figure 2). 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 (Mills 2016, Chandler et al. 2016). Burrowing owls do not breed on the Farallon islands and, by late May, all remaining, surviving owls have departed the island for their breeding grounds (this study). Figure 2 summarizes the annual cycle for each of the three principal species, and linkages among them.

The ultimate goal of our study is to quantify the projected population-level consequences for the storm petrel of a proposed eradication of the mouse (USFWS 2013b). To achieve this goal 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, to characterize the hyper-predation process. (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. Then using the capture-recapture dataset 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. (4) We constructed a population dynamic model that accounts for current population trends, based on our survival estimates, and incorporating data on reproductive success of the Farallon population. We then modeled the future population trajectory of storm petrels considering a range of possible baseline population trends, to understand the change in future population trajectory of storm petrels 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.

In this study, we revise the population-dynamic model developed by Nur et al. (1999a) for this population, analyzing data collected since 2000, while incorporating impacts of burrowing owl predation on storm petrels, which has not been previously addressed for this population. Our analyses focus on estimating the potential effect of owl predation on storm petrel survival during the period, 2000 to 2012. We focus our analyses on the period since 2000

because standardized measures of owl abundance are only available from 2000 on. 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.

METHODS

Phase 1 – Patterns of variation in abundance/ predation rates over time for focal species

This study drew on five main datasets for the three species examined, both for analysis and development of the storm-petrel population dynamic model. These datasets are summarized in Table 1.

House mice abundance.—We created an index of mice 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.

Owl abundance index.—An index of owl abundance was determined based on daily observations of accessible areas from January 2000 to December 2012, supplemented, from 2010 to 2012, by detailed roost surveys of burrowing owls conducted every 3 days during periods of known owl attendance – usually September to May,

depending on arrival and departure of first and last owls. Due to a lack of consistent effort estimating overwintering burrowing owl numbers prior to 2000, the time series analyzed begins in 2000 (Table 1). As part of daily monitoring operations, biologists searched SEFI for all non-breeding terrestrial birds and tallied the total (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), effort was relatively consistent across years. Nevertheless, initiation of color-banding of owls in fall 2007 allowed better subsequent identification of individual owls and their roosts.

We acknowledge this variation in survey effort through time, and 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 for use in these analysis. The index is the maximum number of individual owls seen in a single day, as calculated for each month, determined from daily surveys throughout the time series, and supplemented by roost surveys in recent years. This index better accounted for missed detections on individual daily surveys than did mean monthly values and displayed a higher correlation with the storm petrel predation index (described below) than did the mean or minimum monthly values. 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; about 40% of the South Farallon Islands (including West End Island) are not 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.

Storm petrel predation index. — We developed an index of predation on storm petrels from surveys conducted January 2003 to December 2012. Before 2003, data were not collected in a sufficiently systematic and standardized fashion (Table 1). For each month, we counted the total number of depredated wings based on repeated, standardized 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.

Identified remains were allocated to either predation by western gulls or owls, or were classified as unknown predator. 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 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. There is no evidence to suggest that monthly or annual predation rates on storm petrels differ in surveyed vs. inaccessible areas.

Reproductive success of storm petrels.— Detailed methods to determine storm petrel reproductive success are presented in Appendix S1. Methods generally follow that of Ainley et al. (1990). Mean and between-year variance in reproductive success for 2000-2012 were used in the stochastic population model (details in Appendix S2).

Mist netting of storm petrels.— Standardized mist netting of storm petrels has been conducted in April-August of each year at two sites (Lighthouse Hill [LHH] and Carpenter Shop [CS], Figure 1) since 1992. Here we analyze mist net capture histories of uniquely banded storm petrels from 2000 to 2014. We exclude captures before 2000 for the reasons outlined above. We fit Jolly-Seber models to estimate temporal variation in population size and fit Cormack-Jolly-Seber (CJS) models to estimate adult survival and how that varies over time and with respect to variation in burrowing owl abundance (see details, below). Detailed mist netting methods are included in Appendix S1.

All statistical analyses other than capture-recapture analyses were carried out with STATA 14.2 (StataCorp 2015).

Phase 2 – Estimating change in storm-petrel populations over time using capture-recapture methods

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 change in population size over time, using capture-recapture methods.

For all storm petrel survival and population modelling, we excluded presumed transients from analyses. Transient individuals are those with very low, or zero, site fidelity in contrast to those subadults 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 Jolly-Seber and Cormack-Jolly-Seber (CJS) models and leads to biased estimation of survival (Lebreton et al. 1992). 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 by meeting one of two criteria. The first criterion was if, in any single breeding season, the individual was captured more than once, at least 7 days apart. Alternatively, individuals that did not meet the first criterion were classified as resident if they were captured in more than one year. However, their capture history was only included in the analysis from the year of second capture. Thus, individuals that were caught once and only 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 2017, using the library RMark – Laake et al. 2015) to estimate population size (Cooch and White 2017, chapter 12), based on the capture-recapture data from standardized mist-netting. 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. 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 2017, chapter 12). With Φ , p , $pent$, and N directly estimated, population size in year t (N_t) can then be derived (Cooch and White 2017, chapter 12). As with CJS models, 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 2017, chapter 12). In addition, parameter estimates for individual years may not be adequately estimated in fully time-dependent models. We parametrized the model using capture histories for years 2000-2014, and used POPAN model output to obtain estimated population size for the years 2002-2012, for the reasons described above.

For analyzing population size, we examined models with all possible combinations of full time-dependence for Φ , p , and $pent$. In other words, we compared all models in which zero, one, two, or all three parameters varied among years, where year was treated as a factor. We also included models in which p was potentially a function of netting site. We included site in the estimation of capture probability because the two netting locations differ with regard to habitat features (Sydeman et al. 1998a), which may affect capture probability.

The set of models included alternative parameterizations of Φ and $pent$, each modeled as time-dependent or time-constant; for p , we considered three parameterizations with respect to variation among years (constant, varies with net-hours only, or fully time-dependent) and further that p either varied with site or not. This resulted in a set of 24 models ($2 \times 2 \times 3 \times 2$). Because

our goal with the POPAN model is to determine variation in population size over time, we focused on the fully time-dependent parametrizations described above. The resulting parameters 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).

We used the year-by-year POPAN-derived estimates of population size to characterize population trajectory during the period 2002-2012. Our goal was not to estimate absolute population size, but rather to determine change over time. Here we compared AICc among a set of simple quantitative models and chose a preferred model; all analyses were on ln-transformed values of population size. The set of candidate models examined included Year as linear, quadratic, and cubic polynomial, as well as no trend (slope of zero). In addition, we considered that changes in population trend may have been abrupt rather than gradual (Bestelmeyer et al. 2011). To do this 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, and we thus considered models with knots, which we refer to as change points, at all possible years meeting that requirement: 2005, 2006, 2007, 2008, and 2009. We also considered change points mid-way between the specified years (2005/2006, 2006/2007, etc.). We considered a total of 13 candidate models. The preferred model of population trajectory was then used as a basis for the population dynamic modeling (see below).

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 2000-2012, 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 AICc 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 CJS models (Lebreton et al. 1992, Laake et al. 2015, Cooch and White 2017) using captures from 2000 through 2014. Here, we took a two part approach. Our initial goal was to characterize the change in survival over time. For this we analyzed fully time-dependent CJS models (Lebreton et al. 1992, Cooch and White 2017), similar to that described for population estimation. We considered Φ to either be fully time-dependent or constant. We modelled 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, for the reasons described above. Thus, we compared a set of 12 models (2 alternative parameterizations for Φ x 6 alternative parameterizations for p). As with the POPAN models, we compared models with respect to AICc and the difference in likelihood, and also considered whether all model parameter values were estimable and standard errors could be obtained.

In the second component of survival estimation, 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, and models that included both effects.

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 to 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 (Figure 2). We considered other monthly intervals for this index (e.g., just the months January to April) but results were similar and model fit was poorer using alternative time periods, hence we only present results using the September-April index of owl abundance. Thus, the first year that could be analyzed was 2001 (where owl abundance was estimated for September 2000-April 2001).

When analyzing the effect of owl abundance on storm petrel survival, p was modeled with respect to full-time dependence, netting hours, and/or site, just as was the case with analyzing fully time-dependent survival. For CJS models, we evaluated models with respect to AICc score and estimability of parameters, just as we did with Jolly-Seber models. Thus, our choice of model was based on low AICc score and ability of the model to provide parameter estimates and their standard errors.

Results of the mark-recapture analysis were incorporated into the predictive population dynamic model in two ways (see *Phase 4*, below). 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 and this was used in the population model as described below. Second, we determined the total among-year variation in annual survival and, following Cooch & White (2017), estimated the proportion of variance due to sampling error, with the remaining variance, termed “process

variance” (Gould & Nichols 1998), included in the stochastic modeling (Appendix S2). The fraction of the total process variance due to variation in owl abundance was also estimated (Appendix S2).

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 \hat{c} , and adjust Likelihood Ratio tests accordingly (as described in Cooch and White 2017, chapter 5).

Phase 4: Population modeling of storm petrels for current trends and future population scenarios

Overview and approach used.—To assess and quantify the impact of a change in owl abundance and predation on Farallon storm petrels, a presumed consequence of mouse eradication, we developed a stochastic population dynamic model for the Farallon Island storm petrel population, building on and updating previous work by Nur et al. (1999a).

Our approach was first to construct a stochastic population dynamic model that could best account for the recently observed storm petrel population trend on SEFI, considering evidence from field observations, previous studies, and the scientific literature. The population dynamic model developed yielded a population which, on average, reproduced the empirically observed recent trend, Trend Scenario A, which we refer to as the “observed decline” trend. However, to allow for uncertainty regarding estimates of recent trend and, more importantly, to allow for uncertainty regarding future population trends, we consider two additional baseline trend scenarios. Trend Scenario B was defined as a “moderate decline” and was equal to the estimated slope coefficient of the observed trend plus 1 standard error (i.e., a decline, but of

lower magnitude than the observed decline). Trend Scenario C has a trend equal to the estimated slope coefficient of the observed trend plus 2 S.E.s, resulting in a “nearly stable” population trend. Taken together, Trend Scenarios A, B, and C span a range of plausible future baseline trends to be considered (from 59% decline over a span of 20 years, on average, to a 2.4% increase over 20 years), prior to any actions proposed to reduce owl abundance.

For each trend scenario (A, B, and C), we developed a stochastic population-dynamic model whose mean outcome corresponded to the identified trend for that scenario. To produce the three Trend Scenarios we modified survival of all age classes (juvenile through adult); however, we assumed the same fecundity values applied irrespective of Trend Scenario (i.e., age-specific probability of breeding and reproductive success remained the same). Thus, we assumed that differences in survival alone are sufficient to account for different population trends in the future.

We then incorporated changes in survival rates associated with postulated changes in owl abundance on the Farallon Islands with respect to these three trend scenarios, as determined from our statistical analysis. Thus, we modeled the population dynamics of Farallon storm petrels, given the estimated increases in survival resulting from the postulated reduction in owl predation associated with mouse eradication, with respect to the three examined baseline trend scenarios.

It is possible that potential 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, in the absence of information regarding the magnitude of such an effect, we did not model this pathway, which potentially affects current or future fecundity.

428 *Stochastic population modeling.* —We used RAMAS GIS 5.0 (Akçakaya 2005) to carry
429 out stochastic population modeling. For each Trend Scenario we developed a corresponding
430 Leslie matrix. We assumed that the age structure in the simulation corresponded to the stable age
431 distribution associated with that Leslie matrix. The elements of each Leslie matrix were then
432 modified as described above in relation to presumed reduction of burrowing owl-related
433 mortality as result of reduction in the abundance of owls. We considered three “owl reduction”
434 scenarios (see below) for each baseline Trend Scenario, and thus produced nine Leslie matrices.
435 We then incorporated stochastic variation in fecundity and survival. In each simulation, for each
436 element of the Leslie matrix, RAMAS randomly chose a value drawn from a distribution whose
437 mean was determined as described above and whose SD reflected process variation associated
438 with that parameter (Gould & Nichols 1998; see Appendix S2 for details).

439 *Starting population size.*— Our analysis focused on changes in projected population
440 trends instead of absolute population numbers. Therefore, we depict population modeling results,
441 with and without impacts of mouse eradication, by setting relative population size in “Year 0” to
442 1.0. Thus, projected population size in Years 1 to 20 can be readily compared to Year 0. Year 0
443 corresponds to the year in which owl abundance is first reduced, if it is reduced at all. Reduction
444 in owl abundance is assumed to occur as a result of mouse eradication but we can only speculate
445 as to the rapidity with which owl abundance is affected by the eradication of mice. In the model,
446 storm petrel survival from Year 0 to Year 1 is affected by the postulated change in owl
447 abundance occurring in Year 0.

448 *Population model Leslie matrix: Calibration.*—Reproductive success was based on
449 recent observations in the field (see Appendix S1 for details). Assumptions regarding age-
450 specific survival and breeding probability are described in Appendix S2. For each scenario we

calculated the adult survival rate such that, with the other parameter values fixed, the value used produced a population whose finite population growth rate corresponded to Trend Scenarios A, B, or C. Note that adjustment of adult survival also resulted in proportional adjustment of survival rates of first-year, second-year and third-year individuals; fourth-year individuals were presumed to display adult survival values (Nur & Sydeman 1999; Appendix S2).

Modeling population impacts of owl predation.—After creating the three population dynamic models corresponding to Trend Scenarios A, B, and C, we then projected population change 20 years into the future. This was done assuming that recent baseline survival and fecundity values, in terms of annual mean and standard deviation, will continue unchanged over this period.

Next, we simulated population trajectories over a 20-year period resulting from a change in storm petrel survival, brought about by a postulated 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 years of the time series (2009-2012) to obtain an estimate of more recent owl abundance, which is higher than in the earlier years of the time series, and then consider scenarios in which abundance changes in the future as a result of mouse eradication. We considered two levels of owl abundance reduction for modeling purposes: reducing average abundance by 50% and by 80% compared to the mean observed for the 4 recent years, 5.53. The “80% reduction level” refers to an average reduction in owl abundance in the future, on which basis we have modeled a specified change in storm petrel survival. During the period 2009-2012, the annual owl abundance index varied from 4.5 to 8.25 “owls”, and thus the reduction in owl abundance of 80% (i.e., reduction of 4.42 “owls”) is equivalent to a decrease of between 54% and 98% depending on the year.

In addition, we assumed that first-year and second-year storm petrel survival did not improve as a result of owl reduction, but only survival of third-year and older individuals improved. While age of first breeding is confirmed at age 4, there are little data regarding presence of second- and third-year individuals on the Farallon Islands. For the purposes of modeling, we therefore assumed that second-year birds were absent from the island, but that third-year birds were present and prospecting and that they are as susceptible to predation as are older individuals, following the assumption made by Sydeman et al. (1998a) for this population. Thus, our assumption was intermediate between the two more extreme options of either full susceptibility of second- and third-year individuals to owl predation or no susceptibility of these individuals.

Incorporation of uncertainty into the analyses.— We incorporated uncertainty into the modeling results in three ways: 1) by considering three baseline trends in the absence of impacts of actions directed at altering owl abundance, each with its own associated baseline adult survival value, 2) by considering two different levels of owl reduction, and 3) by incorporating stochasticity of demographic parameters, for both fecundity and survival, in our population modeling, based on the long-term study of storm petrels on the Farallon Islands.

RESULTS

Phase 1 – Patterns of variation in abundance/ predation rates over time for focal species

Monthly variation for the three focal species.—House mice, owl abundance, and storm petrel predation by owls each showed a clear and distinctive seasonal pattern (Figure 3). For mice, the population index was lowest in February-May and highest in August-December (Figure 3; Appendix S3). For owls, the abundance index was high in

October-March and near zero in June-August (Figure 3), 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 (Figure 3). Thus, two temporal trends are of note: 1) the storm petrel predation index increases in January and February and peaks in March, just as the mouse index drops precipitously and storm petrels increase, and 2) at the time that burrowing owls arrive on the island (in September and October), mouse populations are at very high levels (Figure 3). Despite presence of both owls and storm petrels in September and October (Ainley et al. 1990), months that coincide with peak house mouse levels, predation on storm petrels appears to be near zero at this time (Figure 3).

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 ($R^2 = 0.538$; $R^2_{\text{adj}} = 0.502$; $P < 0.0001$, Table 2). After controlling for mouse abundance, there was a highly significant positive relationship between owl abundance and owl predation on storm petrels ($P = 0.001$; Table 2). Likewise, mouse abundance was significantly negatively correlated with the storm petrel predation index, after controlling for owl abundance ($P < 0.001$; Table 2).

Patterns of inter-annual variation in owl abundance and the predation indices are presented in Phase 3.

Phase 2 – Estimating change in storm-petrel populations over time

Storm petrel population size, as determined from POPAN analyses, varied strongly between 2002 and 2012; results of the preferred fully time-dependent model are shown in

Figure 4. To characterize the trajectory over the 11 years, we analyzed 13 models. The two best models, with regard to AICc and estimability of parameters were change-point models. Both models had very similar AICc values (difference of 0.18 units): either a change point in 2005 or mid-way between 2005 and 2006 (i.e., 2005.5). We chose a change point of 2005.5 rather than 2005 because: a) this allowed more data (4 full years) to be used to estimate the slope before the change point, with 7 years post-change point, and b) the population estimates for 2005 and 2006 were very similar, consistent with the assumption that the change in trend occurred between the two years (a difference of 2.3%, which was not significant [$P > 0.5$]; Figure 4). 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. Despite changes in population, reproductive success for SEFI storm petrels was similar between the earlier and later periods (mean = 0.56 [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 a strongly increasing one (29.1%/yr, S.E. = 5.6%, $P < 0.001$; Table 3, Figure 4), followed by a decreasing trend from 2005.5 (4.36%/yr, S.E. = 2.24%, $P = 0.087$). As noted, the difference in trends was significant ($P = 0.001$). Thus, the early 2000's saw a substantial increase in population, a trend that was reversed in the more recent years.

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 (Figure 5A). The overall trend depicted is significant ($P < 0.001$, Table 4A); the best fit, as determined by AICc was a 2-part spline, with a knot at 2006/2007 (Figure 5A, Table 4A). The four years of highest owl abundance have been the four most recent years in the time series (2009-2012). Since 2006/2007, the increasing trend observed is significant ($P < 0.001$, Table 4A); furthermore, the change in trend was significant ($P = 0.023$).

The index of owl predation on storm petrels significantly increased during the same period ($P = 0.006$, Table 4B, Figure 5B). 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 year (S.E. = 5.4%; Table 4B). Thus, over the 9-year span, the trend has been a 250% increase in the predation index (Figure 5B).

Furthermore, the annual storm petrel owl predation index was highly positively correlated with the annual index of owl abundance ($P = 0.003$; $R^2 = 0.740$; $R^2_{adj} = 0.703$). 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, c-hat, of 1.66. While not an excessively large value this

indicated capture heterogeneity and we therefore adjusted Likelihood Ratio (LR) tests using this value of \hat{c} .

Variation in storm petrel survival probability. —Survival estimates showed considerable variation among years (Figure 6A). The difference among years was not significant (LRS = 14.437, df = 10, P = 0.15) after adjusting for capture heterogeneity. As can be seen in Figure 6A, though the magnitude of variation among years was appreciable (estimates varied from 63% to 87%), standard errors for individual years were great. There was a tendency for survival to be higher in the earlier years compared to the more recent years, but there are also exceptions. We were unable to estimate survival in 2005/2006 and 2008/2009 for this model, in which both Φ and p were fully time-dependent, due to insufficient data.

To quantify the relationship of survival to owl abundance, if any, we evaluated a set of competing models. The best-supported model (preferred by AICc) included a linear effect of burrowing owl abundance and the effect of year (as factor) and hours of netting on capture probability (Table 5). A linear effect of owl abundance was preferred over no effect or a quadratic effect. Survival estimates from this model are shown in Figure 6B with respect to year.

More specifically, 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% CI, -0.224 to -0.030; Table 5). Therefore a reduction in the owl abundance index by 50% (i.e., reduction from an index of 5.53 owls to 2.765) is expected to increase logit survival by 0.314. A reduction in the owl index by 80% is expected to increase logit survival by 0.502. The model-based

estimate of annual storm petrel survival is illustrated in Figure 7 with regard to variation in owl abundance.

*Phase 4 - Population modeling of storm petrels for current trends
and future population scenarios*

Population Dynamic Model. —We developed population dynamic models to produce one of three baseline trend scenarios; we refer to the three baseline trend scenarios as Scenarios A, B, and C, respectively. Scenario A was the observed recent decline (at 4.36% per year; see Table 3, Figure 4). Scenario B was a moderate decline, 2.14% per year, while Scenario C was approximately stable at 0.12% increase per year. Adjusted adult survival values, calibrated to produce the specified baseline trends, varied from 0.861 to 0.905 depending on the scenario (Table 6). We then modified survival of all individuals three years and older (see Methods) under the two “burrowing owl reduction scenarios” —50% and 80% reduction—for each of the three baseline trend scenarios.

Adult survival values predicted as a result of a decrease in the owl abundance index are depicted in Table 7. Note that all three trend scenarios modeled (A, B, and C) assume the same change in logit survival as a function of a change in the owl index. However, baseline survival rates differ for the three scenarios and thus the change in survival probability associated with a change in the owl index differs among the scenarios (Table 7).

“Change in Survival” (Table 7) is the projected effect of owl reduction on storm petrel survival. For Scenario A, storm petrel survival is predicted to increase by 3.7 to 5.5% for 50% and 80% owl reduction, respectively. For Scenario C, baseline survival (no owl reduction) is higher than Scenario A (0.905 vs 0.861) and so the increase in survival due to owl reduction is

less, i.e., 2.6 to 3.8%, respectively. Scenario B is intermediate with respect to the effect of owl reduction on storm petrel survival (Table 7).

Simulation results for each of the 9 *trend x owl* reduction scenarios (10,000 simulations per scenario) are summarized in Table 7 and Figures 8, 9, and 10. Lambda values (calculated here as the average annual growth rate over the 20 years of the simulation) are shown in Table 7. Under Scenario A, lambda for the median outcome increases from 0.952 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 or even eliminated with 80% owl reduction. Under Scenario C (nearly stable baseline trend), the median lambda increases from 0.999 to 1.022 and 1.032, respectively. Under this scenario, 80% owl reduction can change a neutral trend to a strongly increasing one.

Expected (median) changes in relative storm petrel population size over a twenty year time period for all three levels of owl reduction (0%, 50% and 80% reduction), and for each population trend scenario, are displayed in Figure 8. Under all three trend scenarios, median results displayed a strong projected effect of owl reduction even after just 10 years. Under Scenario A, future decline is reduced from an expected 38% decline after 10 years, on average, to a 13% decline with 50% owl reduction, and to an expected 2% increase with 80% decline (Figure 8). Similar effects are seen under Scenarios B and C after 10 years (Figure 8). Not surprisingly, impacts of owl reduction are more marked after 20 years. For example, under Scenario B, an expected decline of 40% after 20 years with no owl reduction, is, instead, a 6% or 37% increase with a 50% or 80% owl reduction, respectively (Figure 8). For Scenario C, the expected values based on median outcomes is a 54% or 89% increase after 20 years for 50% or 80% owl reduction, compared to median decline of 1.3% with no owl reduction.

At the same time, a large range of outcomes can be expected for each scenario. Predictions of the stochastic model are illustrated in Figure 9 for the 20 year outcomes and in Appendix S4: Figure S1 for 10 year outcomes; Table 7 provides 5th and 95th percentile lambda values as well, based on 20 year outcomes. Model results demonstrate striking variability of population trajectory across all trend and owl-reduction scenarios. For example, under Scenario A, with no owl reduction the population can be expected to decline by 63% after 20 years. With 50% owl reduction the median expected decline is 26%, but there is a 5% probability that the decline will be 68% or greater while there is also a 5% probability of an increase of 39% or more after 20 years (Figure 9). Thus, while we may expect that a 50% owl reduction may result in a change, on average, from 63% to 26% decline, we may also see a strong decline or a moderately strong increase, though the likelihood of these outcomes is not great. Similar results are seen for the other owl reduction and trend scenarios. This finding underscores the importance of considering the range of outcomes rather than a single expected value. Even after just 10 years, results of the simulations indicate strong variability in outcome (Appendix S4: Figure S1).

The stochastic nature of the expected outcomes is also well-illustrated by considering the probability of population decline after 5, 10, 15, and 20 years (Figure 10). Under Scenario A, there is a 99% probability that the population will have declined to any degree (i.e., 1% probability of stability or growth) after 20 years; however, with 50 and 80% owl reduction, the probability of decline is reduced to 76% and 48%, respectively. Thus, under Scenario A, what was an almost assured population decline is now, with 80% owl reduction, a scenario in which population stability or increase is more likely than population decline. Under Scenario B, 50 and 80% reduction of owl abundance is expected to reduce the probability of storm-petrel population

decline after 20 years from 88% to 44% and 21%, respectively. Similarly strong impacts are seen under Scenario C (Figure 10).

DISCUSSION

We present evidence that annual variation in owl abundance and corresponding predation on ashy storm petrels results in ecologically significant changes in storm petrel survival, which can strongly affect their population trend. Given these impacts, we can expect that, over a broad range of environmental scenarios, a decrease in owl abundance will have significant and positive benefits for Farallon storm petrel population trends. Our results show that even a 50% reduction in owl abundance resulting from a proposed invasive rodent removal can have strong positive population-level impacts across all scenarios addressed, despite substantial uncertainty in outcomes, from reduced declines (Scenario A) to stable (Scenario B) or increasing (Scenario C) storm petrel trends. A postulated reduction of owl abundance by 80% has the potential to produce stable or increasing storm petrel populations on the South Farallon Islands in all three population trend scenarios assessed.

These results provide quantitative evidence supporting the expectation of benefits to the storm petrel population from the proposed mouse eradication on the Farallones. The expected increase in storm petrel survival rates would provide a significant conservation gain for this species. 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 temporal pattern in the monthly data indicates that storm petrels are a secondary prey item for owls. Burrowing owls appear to prefer house mice as prey, but turn to depredating storm petrels when mice abundance has dropped severely (Chandler et al. 2016). This switching

behavior, from a primary to a secondary prey, is consistent with other examples of hyper-predation involving seabird populations on islands (Russell 2011). Both the monthly and annual data demonstrate that the observation of more burrowing owls on SEFI is associated with more predation events on storm petrels by owls. Most importantly, the survival analysis indicates that, on an annual basis, high numbers of burrowing owls in a year are associated with lower adult storm petrel survival. The estimated effect on storm petrel survival of a change in owl abundance was large, especially given that the maximum number of owls recorded in any month was 11 or fewer. For example, under Scenario A, analyses indicated that a 50% reduction in owls is projected to increase storm petrel survival by an absolute 3.7%. This is significant for the population because current annual adult mortality, from all causes, including owl predation, is estimated to be 13.9% under this scenario (Table 7). For a long-lived seabird, such reductions in mortality, in this case from an average of 13.9% to 10.2%, are of great consequence in improving population viability (Weimerskirch 2002, Borrelle et al. 2016).

Our measure of predator abundance is coarse, but provides an index of year to year variation in attendance of burrowing owls on SEFI, and thus of predation risk to storm petrels. We acknowledge that color-banding of owls starting in 2007 has facilitated the tracking of individual birds and that increased daily survey effort beginning in 2010 may influence overall abundance estimates relative to previous years. For this reason, we have used the monthly maximum number of burrowing owls observed on SEFI, which integrates observations over many days and therefore is less sensitive to varying effort or missed detections in any single day. In particular, our results demonstrate a significantly increasing trend in owl abundance since 2007 (when color-banding began), such that numbers observed in 2010-2012 are 160% greater than in 2007-2009 (6.29 ± 1.09 [SE] vs. 2.42 ± 0.44 [SE]; $P = 0.030$).

We note that though the owl abundance index increased from 2006 to 2011 (Figure 5A), the index has stabilized since 2012: the mean abundance index for 2013-2017 (4.65 ± 0.45 [SE]) was very similar to that of 2012 (4.5; Point Blue, unpublished).

The high correlation ($r = +0.860$) observed between the annual index of owl abundance and the annual index of storm petrel predation by owls, an index whose methods have been implemented consistently throughout the 2003-2012 time series, provides additional evidence supporting a causal relationship between variation observed in owl abundance on SEFI and variation in mortality rates of storm petrels. In fact, analysis of annual survival in relation to the storm petrel predation index yields similar results to those presented here with respect to impact of changes in owl abundance: storm-petrel survival to a given breeding season is lower in years with more storm petrel remains depredated by owls, which mainly occurs in the 3 months preceding breeding.

The time series presented here highlight the recent change in the owl abundance index compared to the early-mid 2000's, along with the associated change in the storm petrel predation index. The change in owl abundance trend apparently occurred between 2006 and 2007; subsequently, owl abundance increased, but also showed substantial annual variability (Figure 5A). The change in storm petrel population trend occurred at about 2006. More specifically, 2005 and 2006 were the two years with highest population size, and from 2006 on the population exhibited decline. Thus, the pattern of storm petrel population change and the change in the owl abundance index were approximately concordant. In fact, the storm petrel predation index was moderately high in 2005 (fifth-highest of the 10 years), and thus owl predation on storm petrels during 2005 may have contributed to the change in population trend noted between 2005 and 2006.

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). In addition, gull predation may affect storm petrel survival and population trend. While a reduction in the western gull population observed at the end of the 1990's and into the 2000's may have led to reduced predation rates of gulls on storm petrels, thus contributing to population increase up to 2005, the western gull population has declined in recent years, and thus cannot explain the storm petrel population decline since 2005/2006 (Warzybok et al. 2016).

The recent increase in owl abundance, the parallel increase in the depredated storm petrel remains, and the corresponding significant change in trend of storm petrel population size align with our finding of an effect of owl abundance on storm petrel annual survival, as identified by the capture-recapture analyses. With no change in breeding success through time, it appears the declining population trend is not a result of declining productivity.

While there are no published studies to indicate that the regional population of burrowing owls has changed in size or distribution during the time period studied, we can more directly attribute the change in the owl abundance index to a change in the duration of time that owls stay on the South Farallon Islands (Chandler et al. 2016). Detailed observations 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; mean = 16.2, SD = 2.75; Point Blue, unpublished). From 2008 to 2012, the mean length of stopover per owl (ln-transformed) per year was highly correlated with the annual owl abundance index ($r = +0.965$, $P < 0.01$): the longer, on average, individual owls remain on SEFI, the greater the owl abundance index. This suggests that the increase in the average number of owls observed on SEFI during

748 September – April over the period 2000-2012 can be attributed to the increased length of time
749 that owls are remaining on the South Farallon Islands. We do not have sufficient data to infer
750 whether variation in mouse abundance among years may be influencing stopover duration;
751 trapping success in 2011 was similar to 2001-2004 (Appendix S3), so there is no specific support
752 for this hypothesis.

753 We emphasize that, for storm petrels, the length of time that owls remain on the island is
754 key: the mean arrival date of burrowing owls is 15 October (median 16 October; $n = 182$), with
755 97% of all owls first sighted and identified by the end of November. However, storm petrels do
756 not begin to return to the South Farallon Islands until January, when the first evidence of storm
757 petrel predation has been noted. Thus, there is a two to three month period when owls are not
758 depredating storm petrels but instead relying on mice.

759 Our modeling does not explicitly consider effects of western gull predation on storm
760 petrels, whose overall, population-level impact is similar to that of owl predation, as previously
761 discussed. We acknowledge that predation on storm petrels by western gulls is an important
762 conservation issue that is beyond the scope of this paper. However, per individual, the predation
763 rate by owls on storm petrels is c. 700 to 800 times that of western gulls (Bradley et al. 2011). To
764 reduce gull predation levels on storm petrels by a substantial amount, a very large number of
765 western gulls would likely need to be removed from the island or excluded completely from
766 storm petrel habitat areas. While reducing gull predation would undoubtedly have positive
767 impacts for storm petrel populations, it is not required for the population to switch from decline
768 to stability (Scenarios A and B) or from stability to growth (Scenario C). Our models imply that
769 a substantial reduction in owl predation is sufficient to positively influence storm petrel
770 population trends.

Incorporation of Uncertainty and the Significance of Stochasticity

Ours is a modeling exercise, and thus characterized by several sources of uncertainty. Our objective was to investigate population-level impacts of a change in predation rates associated with reduction in owl abundance and attendance patterns on the Farallon Islands. The first uncertainty concerns what the baseline population trend would be in the future in the absence of owl reduction. We have modeled a range of baseline trends, from a substantial decline to no decline at all. The second uncertainty concerns the degree of owl reduction that results from the proposed mouse eradication: here we have modeled two scenarios, ranging from an average of 50% to 80% reduction of owls. We lack data to model how owls would respond to the elimination of mice as prey, i.e., with regard to the number of owls over-wintering and the duration of stay. We thus consider these two possible levels of owl response and modeled how hypothesized changes in owl numbers affects storm petrel survival. The two levels of reduction thus capture a large amount of uncertainty in the owl response to the mouse eradication.

The third 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). It is therefore important in modeling the potential impact of management actions to incorporate this stochasticity, as we have done here. In our modeling, we first quantified variation in survival among years, and then estimated the proportion due to sampling error, the balance being attributed to process variation (Gould and Nichols 1998). Process variation was a considerable fraction of the total variation for survival, 0.376, and thus the between-year SD for survival due to process variation was substantial, 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. As a result, population trend can show a diversity of results, even under the same baseline trend x owl reduction scenario. Thus, even where population decline is expected, there may be net growth after 20 years and vice versa. For example, under Scenario B (a moderate decline), we expect that 80% reduction will yield, on average population growth (37% increase after 20 years), but there is a 5% probability of population decline of 34% or greater. Quantifying the range of outcomes is an important component in developing and implementing a management strategy for this population.

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 estimates of survival and the effect of burrowing owl abundance on storm petrel survival were based on analyses that excluded transients, i.e., individuals with low site fidelity; exclusion of transients reduced bias and provided for more robust estimates of survival. For population modelling, we addressed uncertainty in storm petrel survival in two ways: (1) The survival values used were calibrated to reproduce one of three population trend scenarios. We allowed for uncertainty in considering future population trends, and therefore we incorporated a corresponding range of adult survival values in our modeling. Baseline adult survival in our population-dynamic modeling varied from 0.861 to 0.905, depending on the trend scenario. (2) The objective of our modeling was to highlight the change in population trend associated with a change in the owl abundance index and therefore a change in predation rates. Our results reveal that the magnitude of the change in 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

baseline survival, ranging from 0.861 to 0.905, is consistent with findings for capture-recapture analyses of the European storm-petrel (*Hydrobates pelagicus*; Sanz-Aguilar et al. 2010, Zabala et al. 2011).

Limitations

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 effects on breeding Farallon storm petrels is minimal (Ainley, et al. 1990). However changes in the seasonal population cycle of mice due to environmental change, such that peak mouse abundances overlapped with peak seabird breeding season, could have substantial impacts on direct impacts of mice on seabirds. This type of event has been observed recently on Midway Atoll, with new records of mice predating adult albatrosses (B. Flint, pers. comm.) 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 effects on storm petrels than we have modeled.

Our projections do not explicitly incorporate impacts of environmental variability on future population trends. The range of baseline population trends considered and the incorporation of stochasticity of demographic parameters presumably reflect future short-term and long-term environmental variability, whose effects are hard to predict. Nevertheless, in the

variable marine environment of the California Current, reduction of predation impacts will surely help storm petrel populations buffer potentially poor oceanic conditions in the future. Long-term persistence of burrowing owls on the Farallones depredating storm petrels will only exacerbate any additional effects on populations due to climate variability.

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, suggest that there will likely be a positive and significant population response by storm petrels and other native species to the removal of invasive rodents (see review in Jones et al. 2011). Analysis of data collected post-eradication will be especially valuable in assessing the assumptions and predictions of the modeling presented here.

Eradication of house mice will not prevent migrating owls from arriving at the Farallon Islands in the fall, primarily in September and October. However, it is likely that the owls would leave soon after arriving if mice are not present and the few chick-rearing storm petrels present would not be enough to sustain the owls. Chandler et al. (2016) showed how during the fall period the biomass of owl diets was almost entirely mice.

Thus, owls would likely not stay several months on the island until storm petrels return in January, as the owls currently do. In particular, there are few or no storm petrels on the Farallon Islands in November and December (Ainley et al. 1990; Point Blue, unpublished). It is not plausible, from an energetics point of view that many owls would continue to stay on the island during those two months and into January in the absence of both their primary prey (house mice)

and their secondary prey (storm petrels). Chandler et al. (2016) showed that, currently, 98.5% of the biomass of prey from burrowing owl pellets is derived from either mice or storm petrels; other prey resources such as insects contributed very little biomass to owl diet and predation on other seabirds by burrowing owls has rarely been observed (Point Blue, unpublished). Even if some owls were able to overwinter on the islands based only on an insect diet, their numbers would likely be much less than their current abundance, as the biomass required to sustain a comparable number of owls would necessitate an increase in insect consumption by several orders of magnitude compared to the present (Chandler et al. 2016).

While it is reasonable to expect that owl predation on storm petrels can be substantially reduced with mouse eradication, eradication may not result in 100% reduction in owl predation on storm petrels. Yet our study has shown that a reduction in owl numbers by 50% can still yield significant positive population level impacts. For owls arriving in September and October there will still be opportunities to prey upon storm petrels, but they are only present in relatively low numbers during those months, compared to their peak abundance earlier in the year. However, if reduction of owl predation could approach 100%, the population response of storm petrels would be even greater than what we have modeled.

This study demonstrates the important role that long term, standardized datasets can play in understanding variation in abundance and behavior of multiple species, thus informing modeling that addresses important conservation and restoration issues. With the many parameters required to model the population response to changes in the predator and prey, it is very valuable to be able to draw on continuous time series, for the many species and populations of interest.

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LITERATURE CITED

- Ainley, D. G. 1995. Ashy storm-petrel (*Oceanodroma homochroa*) in The Birds of North America, No. 185 (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences, Philadelphia, PA and the American Ornithologists Union, Washington, D.C.
- Ainley, D. G., and R. J. Boekelheide, editors. 1990. Seabirds of the Farallon Islands: Ecology, Dynamics, and Structure of an Upwelling-System Community. Stanford University Press, Stanford, CA.
- Ainley, D. G., and K. D. Hyrenbach. 2010. Top-down and bottom-up factors affecting seabird population trends in the California Current System (1985-2006). Progress in Oceanography 84:242-254.
- Ainley, D. G., and T. J. Lewis. 1974. The history of Farallon Island marine bird populations, 1854-1972. Condor 76:432-446.
- Ainley, D. G., R. P. Henderson, and C. S. Strong. 1990. Leach's storm-petrel and ashy storm-petrel. Pages 128-162 in D. G. Ainley and R. J. Boekelheide, editors. Seabirds of the Farallon Islands: Ecology, Dynamics, and Structure of an Upwelling-system Community. Stanford University Press, Stanford, CA.
- Ainley, D. G., N. Nur, J. T. Eastman, G. Ballard, C. L. Parkinson, C. W. Evans and A. L. DeVries. 2013. Decadal trends in abundance, size and condition of Antarctic toothfish in McMurdo, Sound, Antarctica, 1972–2011. Fish and Fisheries 14:343–363.
- Akçakaya, R. 2005. RAMAS GIS: Linking Spatial Data with Population Viability Analysis (version 5). Applied Biomathematics, Setauket, New York.

- 922 Angel, A., R. Wanless, and J. Cooper. 2009. Review of impacts of the introduced house mouse
 923 on islands in the Southern Ocean: Are mice equivalent to rats? *Biological Invasions*
 924 11:1743-1754.
- 925 Bestelmeyer, B. T., A. M. Ellison, W. R. Fraser, K. B. Gorman, S. J. Holbrook, C. M. Laney, M.
 926 D. Ohman, D. P. C. Peters, F. C. Pillsbury, A. Rassweiler, et al. 2011. Analysis of abrupt
 927 transitions in ecological systems. *Ecosphere* 2(12):129. doi:10.1890/ES11-00216.1
- 928 Bolton, M., A. Stanbury, A. Baylis, and R. Cuthbert. 2014. Impact of introduced house mice
 929 (*Mus musculus*) on burrowing seabirds on Steeple Jason and Grand Jason Islands, Falklands,
 930 South Atlantic. *Polar Biology* 37:1659–1668.
- 931 Borrelle, S. B., P. H. Boersch-Supan, C. P. Gaskin, and D. R. Towns. 2016. Influences on
 932 recovery of seabirds on islands where invasive predators have been eradicated, with a focus
 933 on Procellariiformes. *Oryx*, 1-13. doi:10.1017/S0030605316000880
- 934 Bradley, J. S., R. D. Wooller, I. J. Skira, and D. L. Serventy. 1990. The influence of mate
 935 retention and divorce upon reproductive success in Short-tailed Shearwaters *Puffinus*
 936 *tenuirostris*. *Journal of Animal Ecology* 59:487-496.
- 937 Bradley, R., P. Warzybok, D. Lee, and J. Jahncke. 2011. Assessing Population Trends of the
 938 Ashy Storm-petrel on Southeast Farallon Island, California. Report to the US Fish and
 939 Wildlife Service. Point Blue Conservation Science, Petaluma, California. Point Blue/PRBO
 940 Contribution Number 1780.
- 941 Bronson, F. H. 1979. The reproductive ecology of the house mouse. *Quarterly Review of*
 942 *Biology* 54:265-99.
- 943 Brooke, M. D. L, and G. M. Hilton. 2002. Prioritizing the world's islands for vertebrate
 944 eradication programs. *Aliens* 16:12–13.

- 945 Cameron, A. C., and Trivedi, P. K., 1998. Regression Analysis of Count Data. Cambridge
946 University Press, Cambridge.
- 947 Carey, J. R., P. Moyle, M. Rejmanek, and G. Vermeij. 1996. Invasion Biology. Biological
948 Conservation 78:1-213.
- 949 Carter, H. R., W. R. McIver, and G. J. McChesney. 2008. Ashy storm-petrel (*Oceanodroma*
950 *homochroa*) in Shuford, W. D., and T. Gardali, editors. 2008. California Bird Species of
951 Special Concern: A ranked assessment of species, subspecies, and distinct populations of
952 birds of immediate conservation concern in California. Studies of Western Birds 1. Western
953 Field Ornithologists, Camarillo, California, and Calif. Dept. Fish and Game, Sacramento.
- 954 Carter, H. R., D.G. Ainley, S.G. Wolf, and A.M. Weinstein. 2016. Range-wide conservation and
955 science of the Ashy Storm-Petrel *Oceanodroma homochroa*. Marine Ornithology 44:53-62.
- 956 Caswell, H. 2001. Matrix population models. 2nd ed. Sinauer Associates, Sunderland.
- 957 Chandler, S. L., J. R. Tietz, R. W. Bradley, and L. Trulio. 2016. Burrowing owl diet at a
958 migratory stopover site and wintering ground on Southeast Farallon Island, California
959 Journal of Raptor Research 50:391-403.
- 960 Choquet, R., J.-D. Lebreton, O. Gimenez, A.-M. Reboulet, and R. Pradel. 2009. U-CARE:
961 Utilities for performing goodness of fit tests and manipulating Capture-REcapture data.
962 Ecography 32: 1071-1074.
- 963 Cloern, J. E., A. D. Jassby, J. K. Thompson, and K. A. Hieb. 2007. A cold phase of the East
964 Pacific triggers new phytoplankton blooms in San Francisco Bay. Proceedings National
965 Academy of Sciences 104:18561–18565.
- 966 Côté, I. M., and W. J. Sutherland. 1997. The effectiveness of removing predators to protect bird
967 populations. Conservation Biology 11:395-405.

- 968 Courchamp, F., M. Langlais, and G. Sugihara. 2000. Rabbits killing birds: modeling the
969 hyperpredation process. *Journal of Animal Ecology* 69:154-164.
- 970 Cooch, E. G., and G. C. White. 2017. MARK: A Gentle Introduction, 17th Edition. Available at
971 www.phidot.org.
- 972 Cooch, E. G., R. Pradel, and N. Nur. 1996. A Practical Guide to Capture/Recapture Analysis
973 using SURGE. 125 pages. Centre d'Écologie Fonctionnelle et Évolutive - CNRS,
974 Montpellier, France.
- 975 DeCesare, N., M. Hebblewhite, H. S. Robinson, and M. Musiani. 2010. Endangered, apparently:
976 the role of apparent competition in endangered species conservation. *Animal Conservation*
977 13: 353-362.
- 978 DeSante, D. and D. Ainley. 1980. The Avifauna of the South Farallon Islands, California.
979 Studies in Avian Biology No. 4, Cooper Ornithological Society, Lawrence, KS.
- 980 Dilley, B., D. Davies, A. L. Bond, and P. G. Ryan. 2015. Effects of mouse predation on
981 burrowing petrel chicks at Gough Island. *Antarctic Science* 27:543–553.
- 982 Doney, S. C., M. Ruckelshaus, J. E. Duffy, J. P. Barry, F. Chan, C.A., English, C. et al.
983 2012. Climate change impacts on marine ecosystems. *Marine Science* 4:11-37.
- 984 Gervais, J. A., D. K. Rosenberg, and L. A. Comrack. 2008. Burrowing owl (*Athene cunicularia*).
985 in Shuford, W.D. and Gardali T., editors: California Bird Species of Special Concern: A
986 ranked assessment of species, subspecies, and distinct populations of birds of immediate
987 conservation concern in California. Studies of Western Birds 1. Western Field
988 Ornithologists, Camarillo, California, and Calif. Dept. Fish and Game, Sacramento.
- 989 Gould, W. R., and J. D. Nichols. 1998. Estimation of temporal variability of survival in
990 animal populations. *Ecology* 79:2531-2538.

- 991 Grout, D., and R. Griffiths. 2013. Farallon Islands Restoration Project: A report on trials
 992 undertaken to inform project feasibility and non-target risk assessments. Appendix A
 993 in United States Fish and Wildlife Service. 2013. South Farallon Islands Invasive
 994 House Mouse Eradication Project: Draft Environmental Impact Statement. Farallon
 995 National Wildlife Refuge, Fremont CA. Federal register #FWS-R8-NWRS-2013-
 996 0036.
- 997 Harrell Jr, F. E. 2001. Regression Modeling Strategies: With Applications to Linear
 998 Models, Logistic Regression, and Survival Analysis. Springer, New York.
- 999 Haug, E. A., B. A. Millsap, and M. S. Martell. 1993. Burrowing Owl (*Speotyto*
 1000 *cunicularia*), in The Birds of North America (A. Poole and F. Gill, eds.), no. 61,
 1001 Acad. Nat. Sci., Philadelphia.
- 1002 Hilbe, J., 2011. Negative Binomial Regression, 2nd ed. Cambridge University Press,
 1003 Cambridge, UK.
- 1004 Hodges, C. S. N., and R. J. Nagata, Sr. 2001. Effects of predator control on the survival and
 1005 breeding success of the endangered Hawaiian dark-rumped petrel. Studies in Avian Biology
 1006 22:308-318.
- 1007 Howald, G., C. J. Donlan, J. P. Galvan, J. C. Russell, J. Parkes, A. Samaniego, Y. Wang, D.
 1008 Veitch, P. Genovesi, M. Pascal, A. Saunders, and B. Tershy. 2007. Invasive rodent
 1009 eradication on islands. Conservation Biology 21:1258–1268.
- 1010 Irwin, J. 2006. The impact of house mice on ashy-storm petrels on Southeast Farallon Island,
 1011 Unpublished report to U.S. Fish and Wildlife Service. Farallon National Wildlife Refuge,
 1012 Fremont, CA.

- 1013 IUCN. 2017. The IUCN Red List of Threatened Species. Version 2017-3.
 1014 <<http://www.iucnredlist.org>>. Downloaded on 31 March 2018.
- 1015 Jones, H.P., D.R. Towns, T. Bodey, C. Miskelly, J.C. Ellis, M. Rauzon, S. Kress, and M.
 1016 McKown. pp 317-357 in Mulder, C.P.H., W. B. Anderson, D. R. Towns and P. J.
 1017 Bellingham (Eds). Seabird Islands: Ecology, Invasion, and Restoration. Oxford University
 1018 Press, Oxford.
- 1019 Krajick, R. 2005. Winning the war against island invaders. *Science* 310:1410–1413.
- 1020 Kutner, M. H., C. J. Nachtsheim, J. Neter, and W. Li. 2004. *Applied Linear Statistical*
 1021 *Models*. 5th edition. McGraw-Hill/Irwin, New York.
- 1022 Laake, J., E. Rakhimberdiev, B. Augustine, D. Turek, B. Collier, J. Rotella, D. Pavlacky, A.
 1023 Paul, and L. Eberhard-Phillips. 2015. RMark: R Code for MARK Analysis. Version 2.1.14.
 1024 <https://cran.r-project.org/web/packages/RMark/RMark.pdf>.
- 1025 Lebreton, J. D., K. P. Burnham, J. Clobert., and D. R. Anderson. 1992. Modeling survival and
 1026 testing biological hypothesis using marked animals: A unified approach with case studies.
 1027 *Ecological Monographs* 62:67–118.
- 1028 Lee, D. E., N. Nur, and W. J. Sydeman. 2007. Climate and demography of the planktivorous
 1029 Cassin's auklet *Ptychoramphus aleuticus* off northern California: implications for
 1030 population change. *Journal of Animal Ecology* 76:337-347.
- 1031 MacKay, J. W. B., E. C. Murphy, S. H. Anderson, J. C. Russell, M. E. Hauber, D. J. Wilson, and
 1032 M. N. Clout. 2011. A successful mouse eradication explained by site-specific population
 1033 data. pp 198-203 in *Island invasives: Eradication and management*. Veitch, C. R., Clout M.
 1034 N., Towns, D. R., Ed. Gland, Switzerland, IUCN.

- 1035 Martinez-Abraín, A. and D. Oro. 2013. Preventing the development of dogmatic approaches in
 1036 conservation biology: a review. *Biological Conservation* 159:539-547.
- 1037 Mills, K. 2016. Seabirds as part of migratory owl diet on Southeast Farallon Island, California.
 1038 *Marine Ornithology* 44:121-126.
- 1039 Nur, N., and G. R. Geupel. 1993. Evaluation of mist netting, nest-searching and other methods
 1040 for monitoring demographic processes in landbird populations *in* Status and Management of
 1041 Neotropical Migrant Birds (ed. by D. Finch and P. Stangel). USDA Forest Service Gen.
 1042 Techn. Rep. RM-229 pp. 237-244. USDA, Fort Collins, CO.
- 1043 Nur, N., and W. J. Sydeman. 1999. Demographic processes and population dynamic models of
 1044 seabirds: Implications for conservation and restoration. *Current Ornithology* 15:149-188.
- 1045 Nur, N., W. J. Sydeman, D. Girman, T. B. Smith, and D. Gilmer. 1999a. Population status,
 1046 prospects, and risks faced by two seabirds of the California Current: The ashy storm-petrel,
 1047 *Oceanodroma homochroa*, and Xantus' murrelet *Synthliboramphus hypoleucus*. Report to
 1048 U.S. Geological Survey, Biological Resources Division. Available at
 1049 http://www.pointblue.org/uploads/assets/admin/ASSP_and_XAMU_Nur_et_al.1999.pdf
- 1050 Nur, N., S. L. Jones, and G. R. Geupel. 1999b. Statistical Guide to Data Analysis of Avian
 1051 Monitoring Programs. Biological Technical Publication, US Fish and Wildlife Service,
 1052 BTP-R6001-1999.
- 1053 Nur, N., G. R. Geupel, and G. Ballard. 2004. Estimates of adult survival, capture
 1054 probability, and recapture probability: Evaluating and validating constant-effort mist
 1055 netting. *Studies in Avian Biology* 29:63-70.
- 1056 Parker, I. M., D. Simberloff, W. M. Lonsdale, K. Goodell, M. Wonham, P. M. Kareiva,
 1057 M. H. Williamson, B. Von Holle, P.B. Moyle, J.E. Byers, and L. Goldwasser. 1999.

- 1058 Impact: toward a framework for understanding the ecological effects of
 1059 invaders. *Biological Invasions* 1:3-19.
- 1060 Peach, W. J., and S. R. Baillie. 2004. Estimating adult survival rates from between-year
 1061 recaptures in the British Trust for Ornithology Constant Effort Sites Scheme. *Studies*
 1062 in *Avian Biology* 29:71-74.
- 1063 Peterson, W. T., and F. B. Schwing. 2003. A new climate regime in northeast Pacific
 1064 ecosystems. *Geophysical Research Letters* 30:1896, doi:10.1029/2003GL017528.
- 1065 Pradel, R., J. E. Hines, J.-D. Lebreton, J. D. Nichols, and A. Viallefont. 1997. Capture-
 1066 recapture survival models taking account of transients. *Biometrics* 53:60-72.
- 1067 Pyle, P., and R. P. Henderson. 1991. The birds of Southeast Farallon Island: Occurrence
 1068 and seasonal distribution of migratory species. *Western Birds* 22:41-84.
- 1069 R Core Team 2017. R: A language and environment for statistical computing. R
 1070 Foundation for Statistical Computing, Vienna, Austria. URL [https://www.R-](https://www.R-project.org/)
 1071 [project.org/](https://www.R-project.org/).
- 1072 Richardson, T., P. Pyle, R. Burnett, and P. Capitolo. 2003. The occurrence and seasonal
 1073 distribution of migratory birds on Southeast Farallon Island, 1968-1999. *Western*
 1074 *Birds* 34:58-96
- 1075 Russell, J. C. 2011. Indirect effects of introduced predators on seabird islands. pp. 261-
 1076 279 *in* Mulder, C. P. H., W. B. Anderson, D. R. Towns and P. J. Bellingham (Eds).
 1077 *Seabird Islands: Ecology, Invasion, and Restoration*. Oxford Univ. Press, Oxford.
- 1078 Sanz-Aguilar, A., G. Tavecchia, E. Mínguez, B. Massa, F. Lo Valvo, G. A. Ballesteros,
 1079 G. G., Barbera, J. F. Amengual, A. Rodriguez, M. McMinn, M., and D. Oro 2010.

- 1080 Recapture processes and biological inference in monitoring burrow-nesting seabirds.
 1081 J. Ornithol. 151:133–146.
- 1082 Schoener, T. W., and D. A. Spiller., 1996. Devastation of prey diversity by
 1083 experimentally introduced predators in the field. *Nature* 381:691–694.
- 1084 Spear, L. B., T. M. Penniman, J. F. Penniman, H. R. Carter, and D. G. Ainley. 1987.
 1085 Survivorship and mortality factors in a population of Western Gulls. *Studies in Avian*
 1086 *Biology* 10:44-56.
- 1087 Spear, L. B., and D. G. Ainley. 2007. Storm petrels of the eastern Pacific Ocean: Species
 1088 assembly and diversity along marine habitat gradients. *Ornithological Monographs*. 62.
- 1089 StataCorp. 2015. *Stata Statistical Software: Release 14*. StataCorp LP, College Station, TX.
- 1090 Sydeman, W. J., N. Nur, E. B. McLaren, and G. J. McChesney. 1998a. Status and trends of the
 1091 ashy storm-petrel on Southeast Farallon Island, California, based upon capture-recapture
 1092 analyses. *Condor* 100:438-447.
- 1093 Sydeman, W. J., N. Nur, and P. Martin. 1998b. Population viability analyses for endemic
 1094 seabirds of the California marine ecosystem: the ashy storm-petrel (*Oceanodroma*
 1095 *homochroa*) and Xantus' murrelet (*Synthliboramphus hypoleucus*). Report to U.S.
 1096 Biological Resources Division, Species at Risk Program. Point Blue Conservation Science,
 1097 Petaluma, California.
- 1098 Towns, D.R., G. V. Byrd, H. P. Jones, M. J. Rauzon, J. C. Russell , and C. Wilcox. 2011.
 1099 Impacts of introduced predators on seabirds. pp 358-392 *in* Mulder, C.P.H., W. B.
 1100 Anderson, D. R. Towns and P. J. Bellingham (Eds). *Seabird Islands: Ecology, Invasion, and*
 1101 *Restoration*. Oxford University Press, Oxford.

- 1102 United States Fish and Wildlife Service. 2009. Endangered and threatened wildlife and plants;
 1103 12-month finding on a petition to list the Ashy Storm-petrel as threatened or endangered.
 1104 Notice of 12-month petition finding. Federal Register 74:41832-41860.
- 1105 United States Fish and Wildlife Service. 2013a. Endangered and Threatened Wildlife and Plants;
 1106 12-Month Finding on a Petition to List the Ashy Storm-petrel as an Endangered or
 1107 Threatened Species. Federal Register Document 2013-24170. Sacramento, CA.
- 1108 United States Fish and Wildlife Service. 2013b. South Farallon Islands Invasive House Mouse
 1109 Eradication Project: Draft Environmental Impact Statement. Farallon National Wildlife
 1110 Refuge, Fremont CA. Federal register #FWS-R8-NWRS-2013-0036
 1111 <http://www.regulations.gov>
- 1112 Wanless, R., A. Angel, R. Cuthbert, G. Hilton, and P. Ryan. 2007. Can predation by invasive
 1113 mice drive seabird extinctions? *Biology Letters* 3:241-244.
- 1114 Wanless, R. M., N. Ratcliffe, A. Angel, B.C. Bowie, K. Cita, G. M. Hilton, P. Kritzing, P. G.
 1115 Ryan, and M. Slabber. 2012. Predation of Atlantic Petrel chicks by house mice on Gough
 1116 Island. *Animal Conservation* 15:472-479.
- 1117 Warzybok, P.M., R. Berger, and R.W. Bradley. 2016. Population Size and Reproductive
 1118 Performance of Seabirds on Southeast Farallon Island, 2016. Report to the U.S. Fish and
 1119 Wildlife Service. Point Blue Conservation Science, Petaluma, California. Point Blue
 1120 Conservation Science Contribution Number 2103.
- 1121 Weimerskirch, H. 2002. Seabird demography and its relationship with the marine environment
 1122 pp. 115-136 in *Biology of Marine Birds*, E. A. Schreiber and J. Burger (Eds.). CRC Press,
 1123 Boca Raton.

- 1124 Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying
1125 threats to imperiled species in the United States. *Bioscience* 48:607–615.
- 1126 Zabala, J., I. Zuberogitia, J. A. Martínez-Climent, and J. Etxezarreta, 2011. Do long
1127 lived seabirds reduce the negative effects of acute pollution on adult survival by
1128 skipping breeding? A study with European storm petrels (*Hydrobates pelagicus*)
1129 during the *Prestige* oil-spill. *Mar. Pollut. Bull.* 62:109–115.
- 1130 Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed
1131 effects models and extensions in ecology with R. Springer, New York.
- 1132

1133 **Table 1.** Summary of datasets used in this study.

Dataset	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; detailed roost surveys began 2010
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	Annual	2000-2012	Used annual means and SEs for to estimate mean and variance in stochastic population model

Table 2. Regression analysis of storm petrel predation index (ln-transformed), by month, in relation to mouse and owl monthly abundance indices. Number of observations = 29. Test of overall model: $F(2,26) = 15.12$; $P < 0.001$. $R^2 = 0.538$, $R^2_{adj} = 0.502$. See text for definition of each index.

Variable	Coefficient	S.E.	t	P value
Mouse trapping index	-3.463	0.674	-4.96	$P < 0.001$
Owl abundance index	+0.199	0.056	+3.55	$P = 0.001$
Intercept	+1.745	0.301	+5.80	$P < 0.001$

1141 **Table 3.** Analysis of population change over time for ashy storm-petrels on Southeast Farallon
 1142 Islands, based on POPAN modeling. Preferred model for change over time is linear spline model
 1143 with change point midway between 2005 and 2006 (see text, Figure 4). Based on analysis of
 1144 individual year estimates from preferred POPAN model (where Φ : time-dependent; p : site +
 1145 hours + time-dependent; ρ : time-dependent; N : site). Dependent variable is $\ln(\text{population}$
 1146 $\text{size})$, from POPAN, weighted by the inverse of the standard error of the estimate. Number of
 1147 observations = 11. $F(2,8) = 18.82$; $P < 0.001$. $R^2 = 0.825$; $R^2_{\text{adj}} = 0.781$, $AIC_c = -9.277$.

Variable	Coefficient	S.E.	t statistic	P value
Year: to 2005.5	+0.2552 ¹	0.0436	5.85	$P < 0.001$
Year: from 2005.5	-0.0446 ¹	0.0229	-1.95	$P = 0.087$

1148 ¹- Test of differences in year-trend coefficients: Up to 2005.5 vs Since 2005.5: $F(1,8) = 24.96$; P
 1149 $= 0.001$.

1150

1151 **Table 4.** Trends of owl abundance and predation on storm petrels among years.

1152 **A.** Preferred statistical model for owl abundance index (ln-transformed) in relation to year, as
 1153 identified by AICc, 2001 to 2012. Number of observations = 12. $F(2,9) = 18.92$; $P < 0.001$. $R^2 =$
 1154 0.808 ; $R^2_{adj} = 0.765$, $AICc = 12.420$.

Variable	Coefficient	S.E.	P value
Year: to 2006/2007	-0.001 ¹	0.061	$P > 0.9$
Year: from 2006/2007	0.298 ¹	0.061	$P < 0.001$

1155 ¹- Test of differences in year-trend coefficients: Prior to 2006/2007 vs Since 2006/2007: $F(1,9) =$
 1156 7.53 ; $P = 0.023$.

1157

1158 **B.** Preferred statistical model for owl predation index (ln-transformed) in relation to year, as
 1159 identified by AICc, 2003 to 2012. Number of observations = 10. $F(1,8) = 14.01$; $P = 0.006$. $R^2 =$
 1160 0.637 ; $R^2_{adj} = 0.591$, $AICc = 10.241$.

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

1161

Table 5. Ashy storm-petrel survival analysis using MARK. Analysis for Southeast Farallon Island, capture histories, 2000-2014. Parameter estimates and Likelihood Ratio Tests (LRTs) for top survival model (AICc preferred). Model: Φ as a function of linear owl abundance index; p a function of year (as factor) + netting hours. Year-specific parameter values for p are not shown in the Table (see footnote 2). Likelihood Ratio Statistics (LRSs) are included at the foot of the Table; LRS and P values are adjusted for goodness of fit ($\hat{c} = 1.66$). AICc = 2591.08, Log likelihood = -2556.64.

Parameter	Estimate	St. Error	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

¹ - LRT for effect of owl abundance on Φ , LRS = 3.31, df = 1, P = 0.069.

² - LRT for effect of full-time dependence on p, compared to constant p, LRS = 33.04, df = 13, P = 0.002.

Table 6. Ashy storm-petrel demographic parameter values used to model projected conditions with no owl reduction. Three different baseline scenarios are modeled: A) “Observed Decline”; B) “Moderate Decline”; and C) “Near-Stable”; see text and Appendix S2.

Age	Survival Relative to Adult ¹	Scenario A Survival ²	Scenario B Survival ²	Scenario C Survival ²	Breeding Proba- bility ³	Repro- ductive Success ⁴
1	0.72	0.620	0.636	0.651	0	0
2	0.86	0.740	0.759	0.778	0	0
3	0.98	0.844	0.865	0.887	0	0
4	1	0.861	0.883	0.905	0.092	0.610
5	1	0.861	0.883	0.905	0.460	0.610
6	1	0.861	0.883	0.905	0.828	0.610
7-15	1	0.861	0.883	0.905	0.920	0.610
16+	0.95	0.818	0.839	0.860	0.920	0.610

¹ - Nur et al. 1999a

² - Adult survival calibrated for that scenario; see text.

³ - Fraction of individuals breeding for age class, either for first time or as experienced breeders; same value for all trend scenarios.

⁴ – Mean value, SEFI, Appendix S2; same value for all trend scenarios.

Table 7. Predicted impact of a change in burrowing owl abundance on Southeast Farallon Island on ashy storm-petrel survival and projected population growth rate. Three baseline scenarios are considered: A) Observed recent decline, B) Moderate decline, and C) Near-stable; see text and Table 6. For each trend scenario, 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 (λ), as determined from median, 5th, and 95th percentile simulation results at year 20 are shown.

A: “Observed Decline”

Change in Owl Abundance Index	Adult Survival	Change in Survival	Lambda (median)	5th -95th percentile Lambdas
0	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

1189 **Table 7 cont.**

1190 **B: “Moderate Decline”**

Change in Owl Abundance Index	Adult Survival	Change in Survival	Lambda (median)	5th -95th percentile Lambdas
0	0.883	0	0.975	0.934, 1.009
50% Decrease	0.914	0.031	1.003	0.965, 1.037
80% Decrease	0.930	0.047	1.016	0.979, 1.045

1191

1192 **C: “Near-Stable”**

Change in Owl Abundance Index	Adult Survival	Change in Survival	Lambda (median)	5th -95th percentile Lambdas
0	0.905	0	0.999	0.959, 1.030
50% Decrease	0.931	0.026	1.022	0.985, 1.050
80% Decrease	0.943	0.038	1.032	0.998, 1.058

1193

1194

Figure Legends

Figure 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 = Ashy storm-petrel. Inset depicts general location of the Farallon Islands relative to San Francisco. Contour interval is 40 feet (12.19 m).

Figure 2. Conceptual diagram of annual cycle. Annual cycle from January through December for all three species. Innermost circle, month. Second circle (red), mice. Third circle (black) variation in storm petrel predation. Fourth circle (green), variation in owl behavior and abundance. Outermost circle (purple) variation in storm petrel attendance and behavior.

Figure 3. Monthly variation in three key metrics: mouse abundance index (2001-2004, 2011-2012; in red), index of storm petrel predation by burrowing owls (2008-2012; in black), and burrowing owl abundance index (2008-2012; in green) at Southeast Farallon Island. Mean monthly mean values and standard deviations are shown.

Figure 4. 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 2000-2013. Estimates for 2002-2012 are depicted; POPAN is not able to estimate population size in 2000, 2001, or 2013 (see text). Also depicted is the trend over trend-over-time model, a linear spline with change point at 2005/2006; see Table 3.

Figure 5. A) Variation in the annual burrowing owl abundance index for 2001 to 2012 on Southeast Farallon Island. Note that mean for September 2000 to April 2001 is shown as “2001”, etc. The abundance index was ln-transformed for analysis; the curve of best fit as determined by AICc, 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

1218 “knot” between 2006 and 2007 (Table 4A). **B)** Annual index of burrowing owl predation on
 1219 storm petrels from 2003 through 2012 on Southeast Farallon Island (monthly mean for January-
 1220 December in each year). The predation index was ln-transformed for analysis; the curve of best
 1221 fit, was determined by AICc. Shown is the back-transformed best fit, a constant proportional
 1222 change from 2003 to 2012 (Table 4B).

1223 **Figure 6.** Annual survival estimates for ashy storm-petrels on SEFI. Survival to the listed year is
 1224 depicted (e.g., “2002” refers to survival from 2001 to 2002). **A)** Survival estimates by year from
 1225 the fully time-dependent model with 95% CIs. Program MARK could provide no estimates for
 1226 2005/2006 and 2008/2009 for this model. **B)** Survival estimates by year from the model for
 1227 burrowing owl abundance (Table 5) shown in black, with 95% CIs. The fully time-dependent
 1228 survival estimates (see panel A) are depicted in red to facilitate reference.

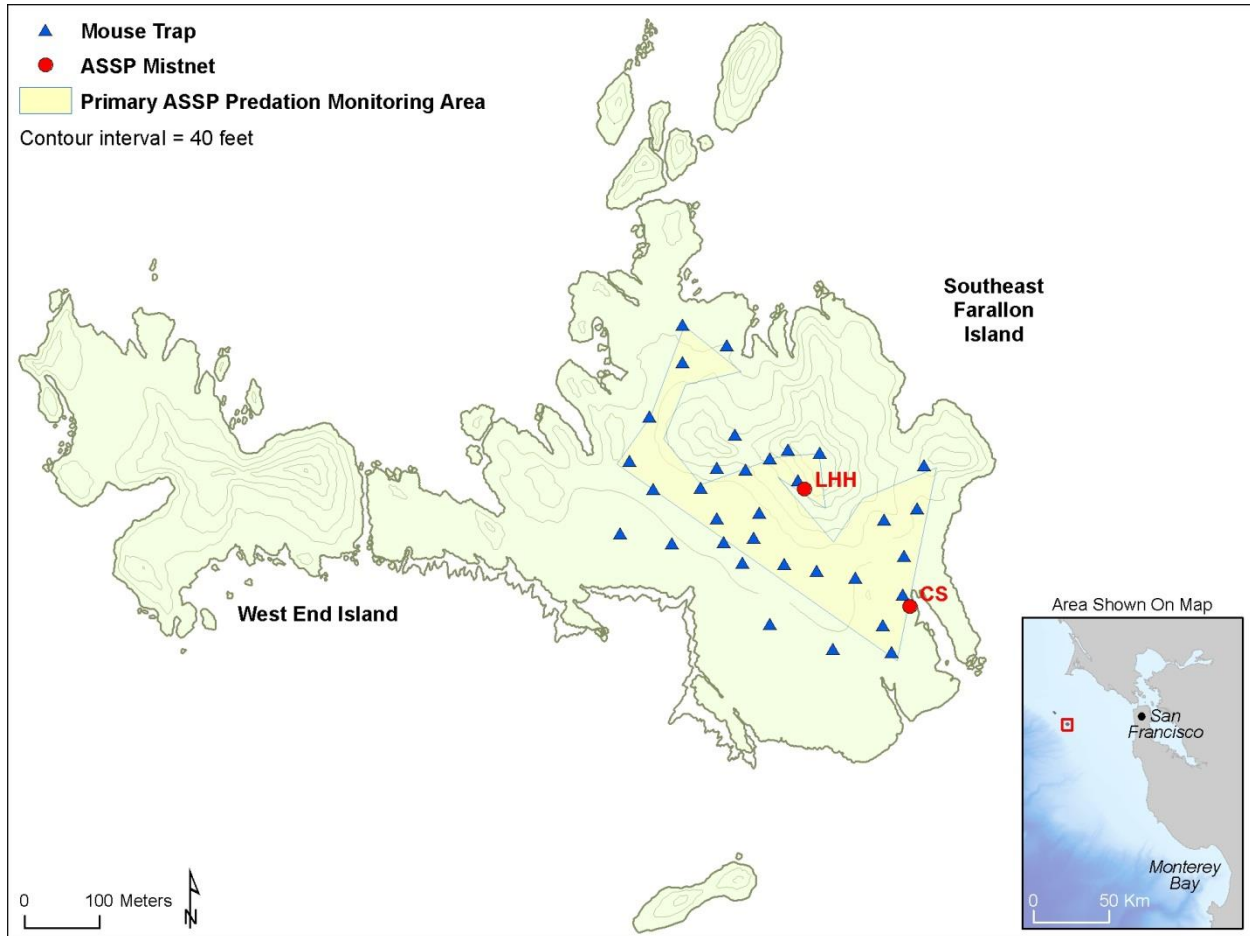
1229 **Figure 7.** Ashy storm-petrel adult survival as predicted by burrowing owl abundance model, for
 1230 survival, as estimated for 2000/2001 to 2011/2012 (see Table 5). Model-predicted survival
 1231 values are shown in relation to the burrowing owl abundance index for that year.

1232 **Figure 8.** Farallon ashy storm-petrel population projections under the three levels of reduction
 1233 in burrowing owl abundance: 0% reduction (black circles), 50% reduction (red triangles), and
 1234 80% reduction (green squares). Median results from simulations (10,000 simulations per trend-
 1235 owl reduction scenario combination) are shown. Levels of reduction are modeled for each of
 1236 three baseline trend scenarios: **A)** “Observed Decline”; **B)** “Moderate Decline”; and **C)** “Near-
 1237 Stable” (see Table 7). Depicted are relative population sizes for a 20-year period; the population
 1238 size index has been set to 1.0 for Year 0. Year 0 corresponds to the year in which burrowing owl
 1239 reduction is implemented, hence the storm petrel population is assumed to first respond between
 1240 Year 0 and Year 1.

1241 **Figure 9.** Farallon ashy storm-petrel simulation results illustrating stochastic variation in
1242 outcomes for the three trend scenarios (each with three owl reduction scenarios: 0, 50, and 80%)
1243 after 20 years (10,000 simulations for each trend-owl reduction combination). From top to
1244 bottom: 95th percentile outcome (green triangle), 75th percentile (red x), median (filled black
1245 circle), 25th percentile (red x), and 5th percentile (green triangle).

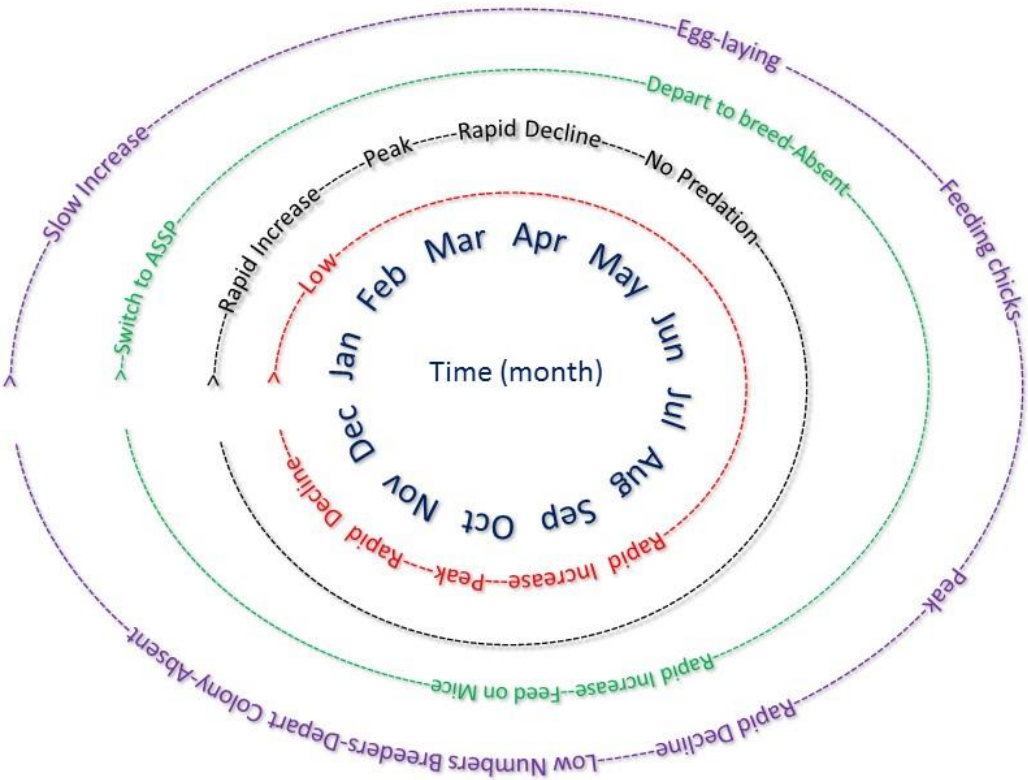
1246 **Figure 10.** Probability of population decline for the Farallon ashy storm-petrel population under
1247 three levels of reduction in burrowing owl abundance (0, 50, and 80%) and with respect to three
1248 baseline trend scenarios: **A)** “Observed Decline”; **B)** “Moderate Decline”; and **C)** “Near-Stable”.
1249 Depicted is the probability of a net decline at the end of 5, 10, 15, and 20 years, respectively.

1250

Fig 1

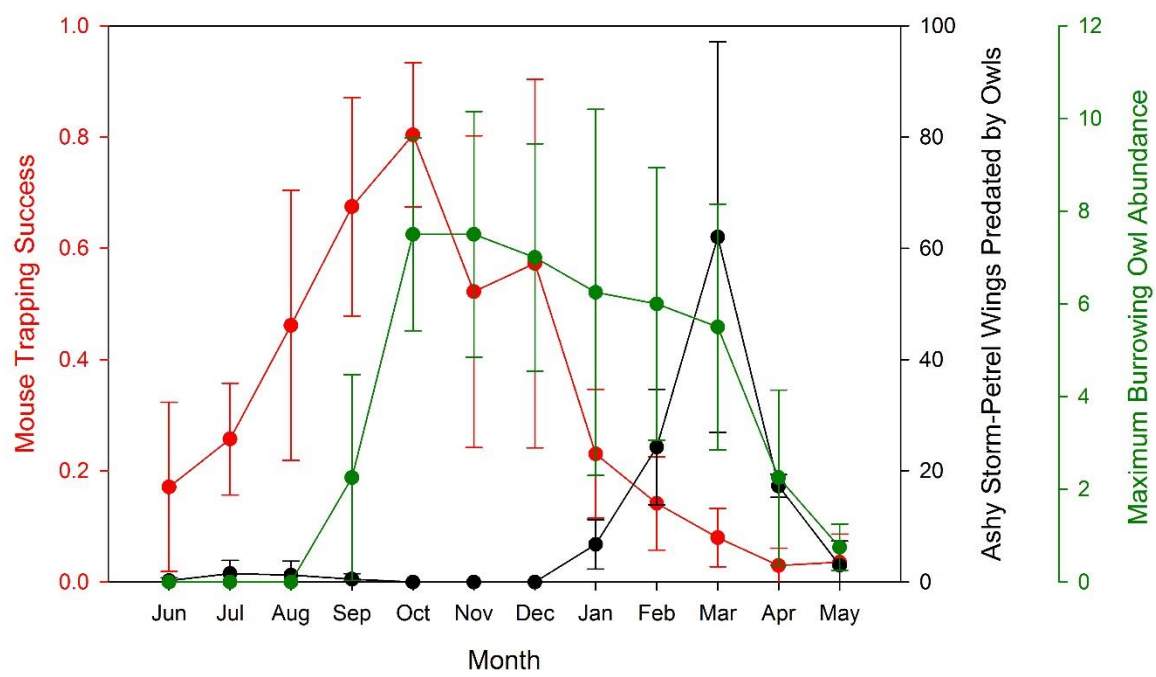
1254 **Fig 2**

Mouse abundanceBurrowing Owl predation on storm petrels



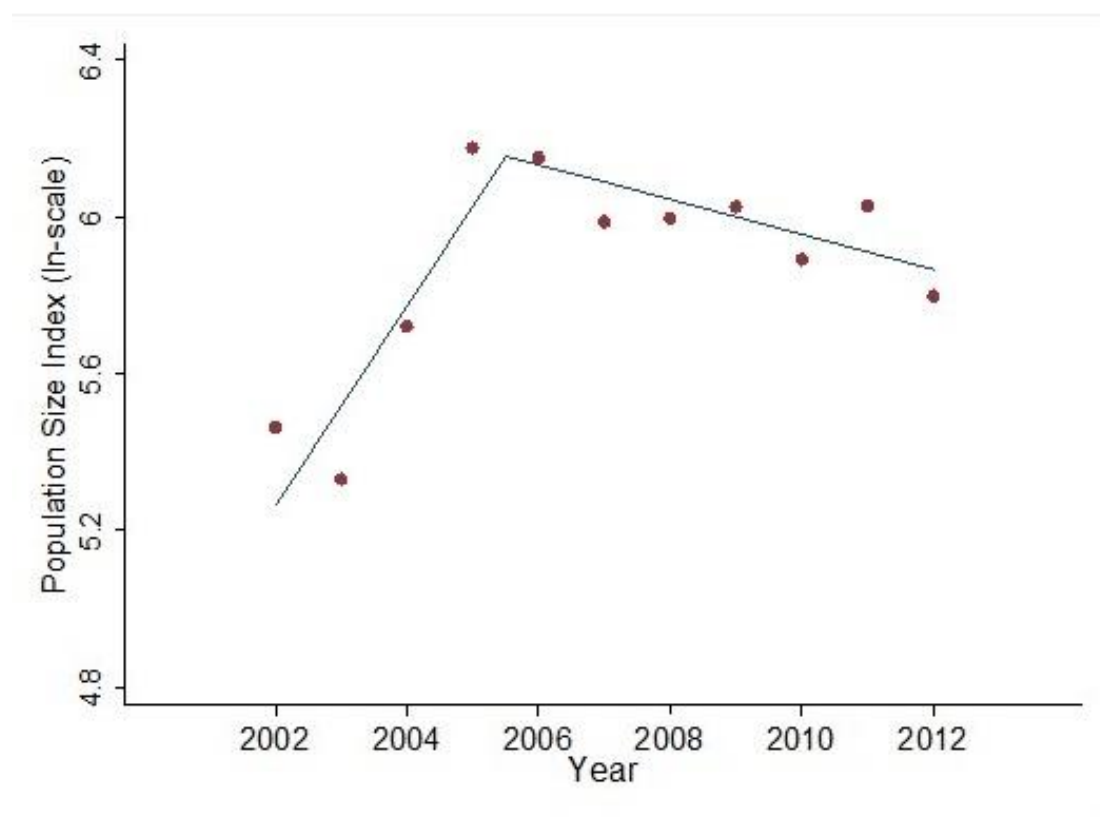
1255 Ashy Storm-Petrel abundanceBurrowing Owl abundance and behavior

1256 **Fig 3**



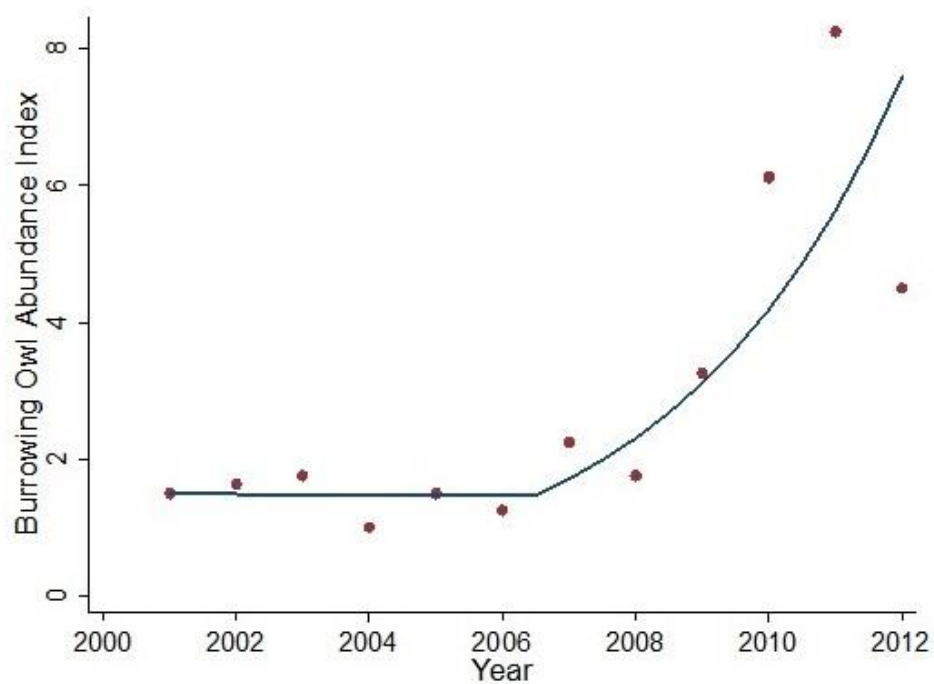
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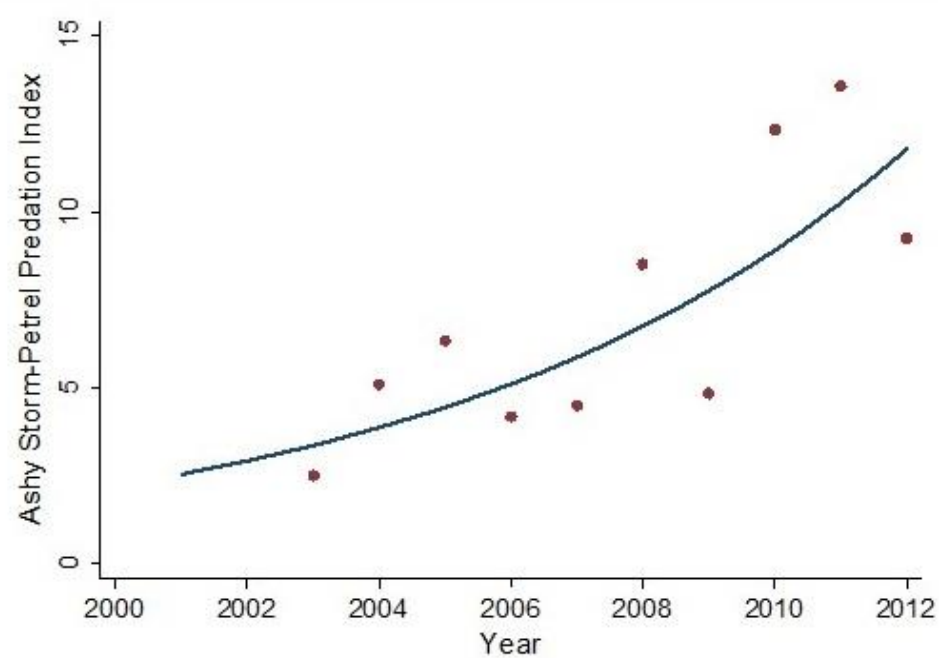
1259 **Fig 4**

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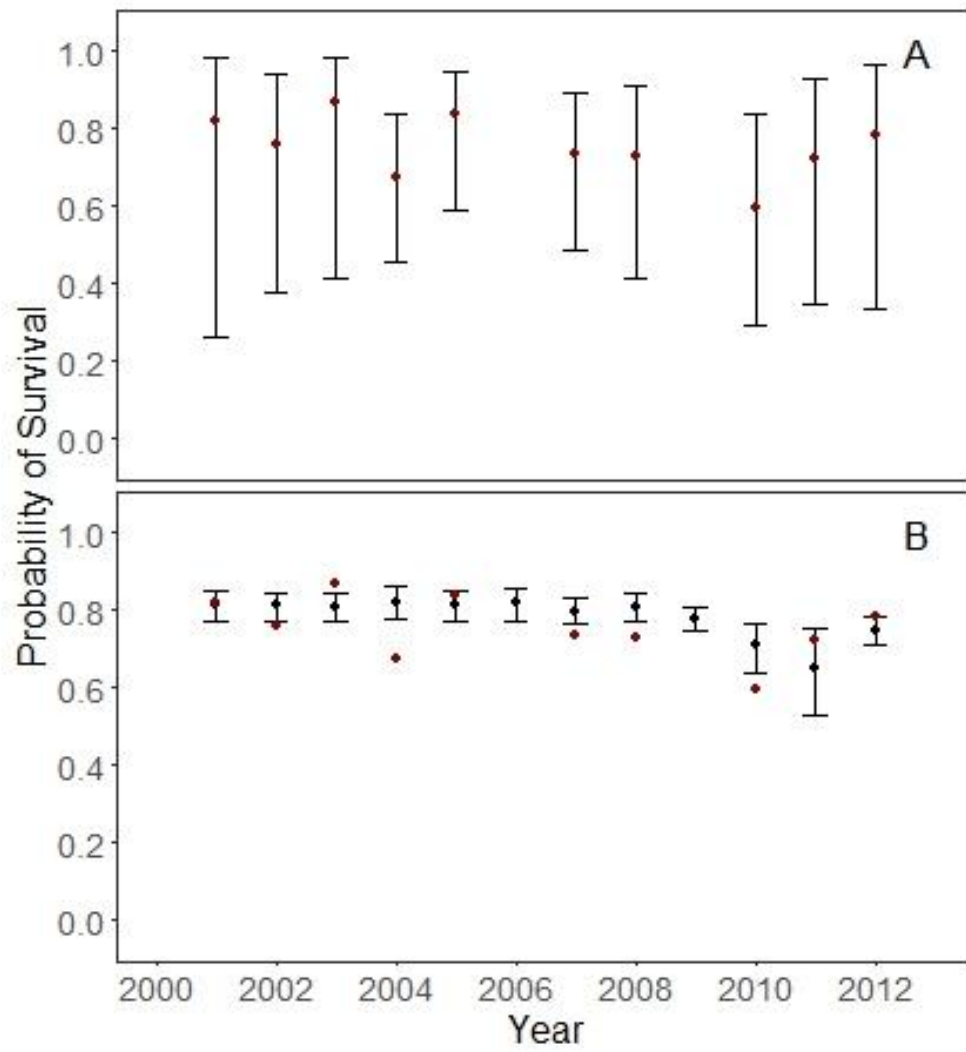
1262 **Fig 5**1263 **A**

1264

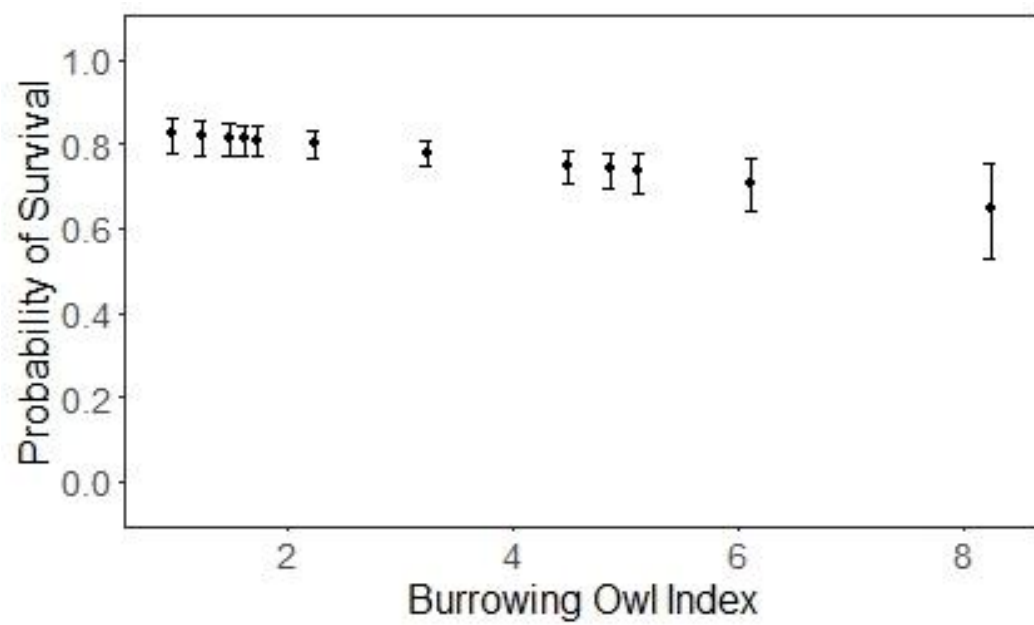
1265 **B**

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1267

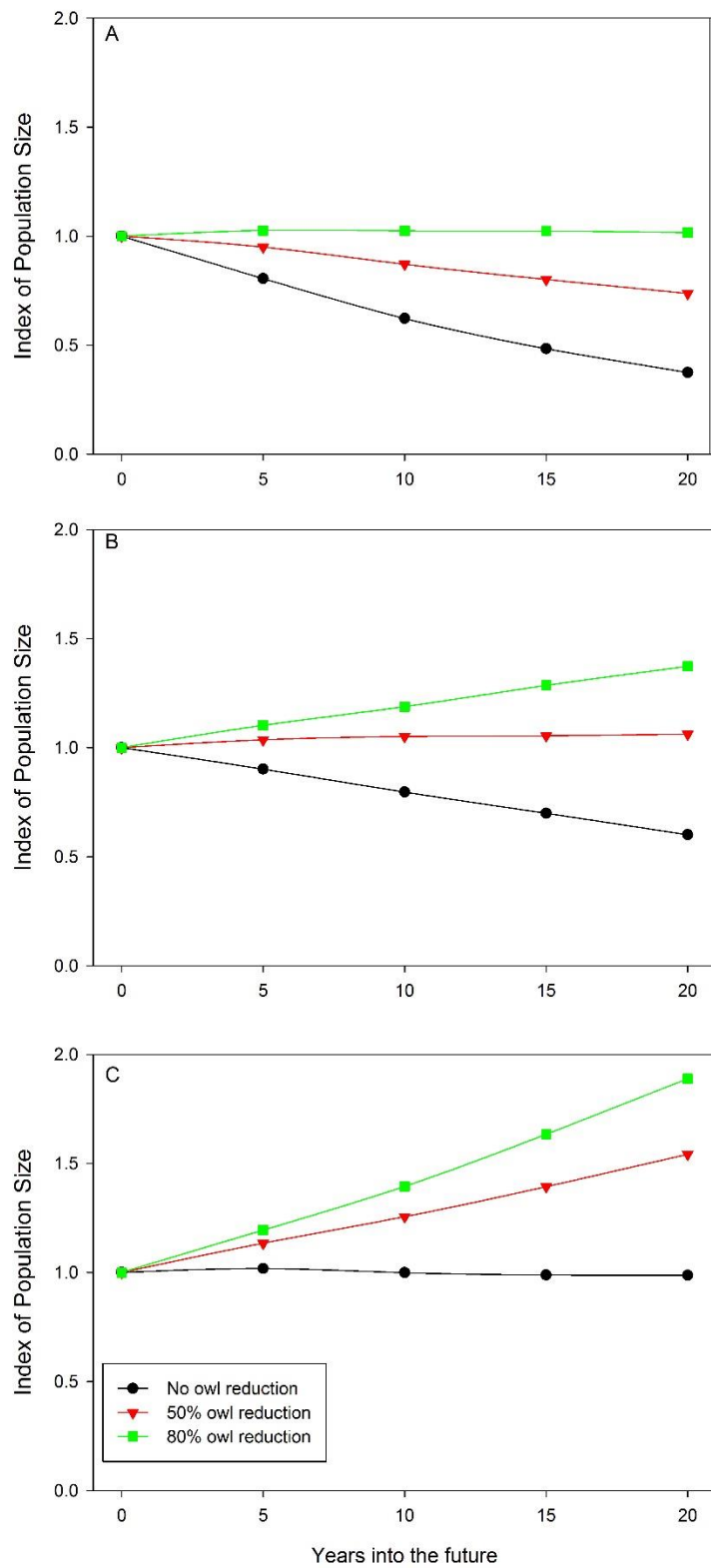
1268 **Fig 6**

1269

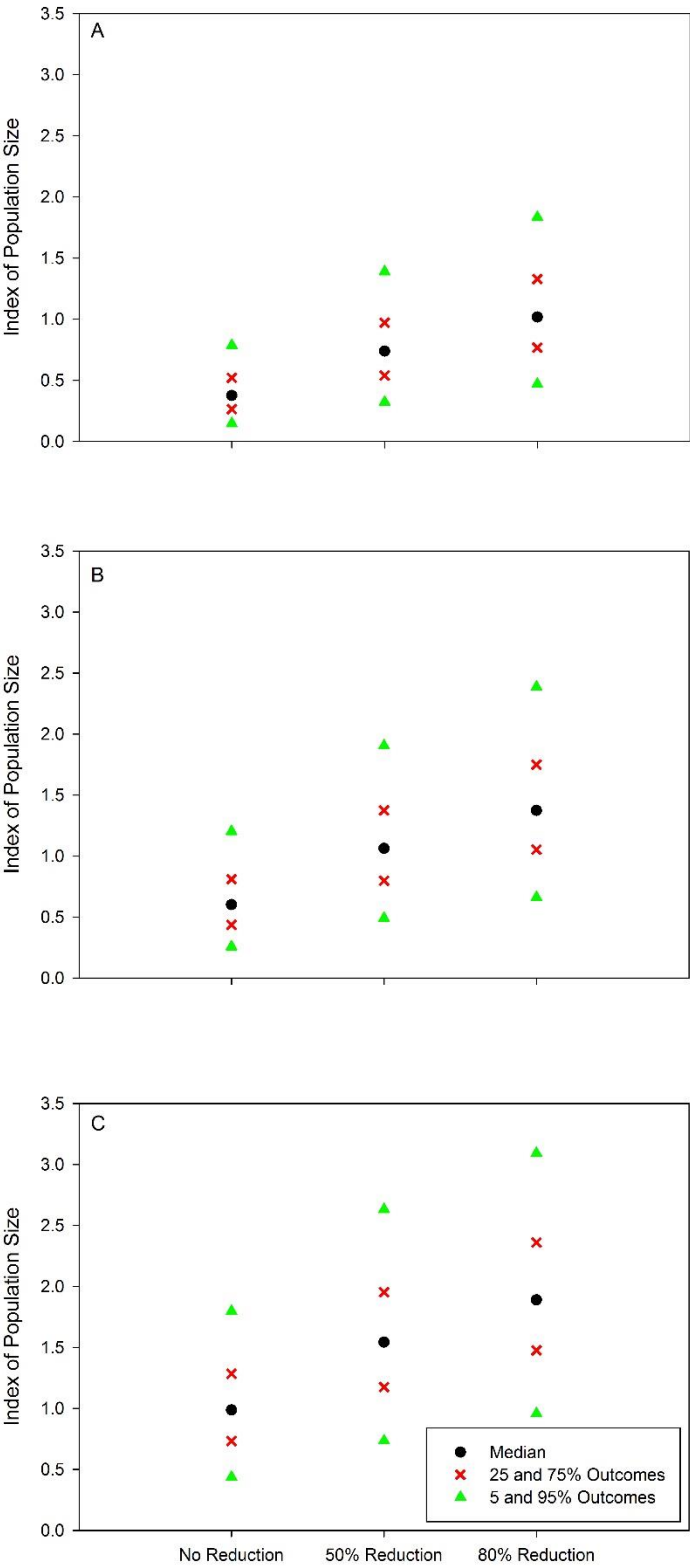
1270 **Fig 7**

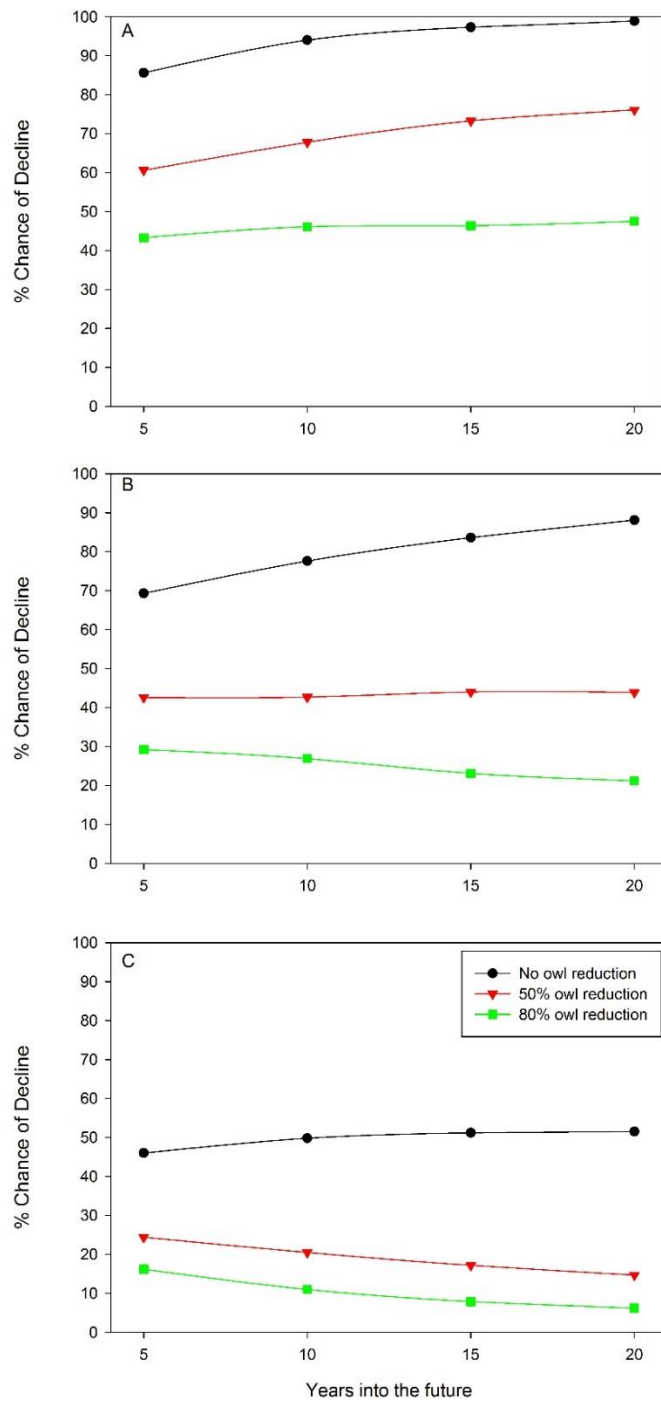
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1273 **Fig 8**

1275 **Fig 9**



1277 **Fig 10**

Supporting Information

Appendix S1. Detailed Field Methods

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 1992-2012, as well as matching periods of regular storm petrel colony

1305 attendance (Ainley et al. 1990). Egg-laying by ashy storm-petrels typically commences in May
1306 (Ainley et al. 1990).

1307 Social attraction, in the form of broadcast recordings of ashy storm-petrel calls, was used during
1308 all net sessions to increase the chance of ashy storm-petrel captures at the netting sites. A
1309 portable cassette tape player (1992-2007) or digital music player and speaker (2008-2012) was
1310 placed at the base of the middle of the mist net and broadcast at a volume of ~65db throughout
1311 the netting sessions. The main calls on the tape were “flight calls,” but in the background low
1312 frequency burrow “purring calls” and “rasping calls” are also present (Ainley 1995). The flight
1313 call rate was approximately 0.44 calls per second or 26.5 calls per minute.

1314

1315 *Methods for Determining Storm Petrel Reproductive Success*

1316 Beginning 5 May in each year, we checked all previously occupied breeding sites every 5 days to
1317 determine nest contents. All occupied sites were monitored for reproductive success, with a goal
1318 of at least 40 sites monitored each season. Sites that had not been occupied for at least 5
1319 consecutive years were dropped from further study. We used a flashlight and, starting in 2007, a
1320 small video inspection camera (“See Snake®” RIGID Tools) to thoroughly examine each site.
1321 The camera allowed for increased sample size from 2007-2012, doubling the number of active
1322 sites we could follow. Once an egg was found or an adult was observed in incubation posture for
1323 two consecutive checks, the site was left undisturbed for 40 days before returning to check for
1324 hatch. Once a hatched chick was confirmed, the site was left undisturbed for an additional 40
1325 days. After the second “skip” period, we resumed checking the site every five days until the
1326 chick fledged. The two “skip” periods helped reduce potential disturbance to incubating adults
1327 and young chicks. Chicks that were fully feathered and disappeared from their nesting crevice

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1328 after 60 days of age were assumed to have fledged (Ainley et al. 1990). In the absence of other
1329 data we assume similar reproductive success between accessible and inaccessible habitats.
1330 Clutch size is 1; storm petrels can relay after failed breeding attempts (Ainley 1995).
1331 Reproductive success was determined with respect to all attempts of a pair (including relays).
1332

Appendix S2. Construction of the Population Dynamic Model

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.

i) **Survival of adults.** Nur et al. (1999a) 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 juveniles to produce three trend scenarios: (A) a population that exhibited the same population trajectory as has recently been observed (a decline of approximately 4.34% per year, see “Results”), (B) a moderate decline of approximately 2.14% per year, and (C) a nearly stable population 0.12% increase per year).

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; 2017). The stochastic model incorporated the among-year SD of the biological process variation using program RAMAS (Akçakaya 2005).

Furthermore, we partitioned the between-year process variance into that due to variation in burrowing owls and process variance not due to owls. To estimate the fraction of the

total process variance due to annual variation in owls, 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”, which is also equal to the ratio of the respective Likelihood Ratio Statistics (that is, LRS for a model with linear fit for owl abundance divided by LRS for a model with full time-dependence) was used to estimate the proportion of total process variance due to owls. This estimate of between year variance due specifically to owls was adjusted in relation to the presumed reduction in owl abundance. Thus, a 50% reduction in owl abundance was assumed to reduce between-year variance due to owls by 50%, but leave the other component of process variance unchanged.

ii) **Survival of juveniles and subadults.** We followed Nur et al. (1999a) 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. (1999a) were: 72%, 86%, and 98% of the adult value. The adult survival value, in turn, depended on the baseline trend scenario, as well as potential effects of owl reduction. By the fourth year of life, ash 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 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 survival was scaled up or down with respect to the three baseline trend scenarios as well as changes in survival 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, 2017), and from that derived the appropriate SD. We had not information to indicate that reproductive success among those that bred varied with age, and so assumed age-constancy.

Note that the same reproductive success values (with regard to mean and SD) were used for all scenarios.

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. (1999a) 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. (1999a) who drew

on a field study of the closely related Leach's storm-petrel (*O. leucorhoa*, Huntington et al. 1996). Nur et al. (1999a) 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, our model assumes 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. 1999a, 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 wide-ranging 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 which 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 (Mainwood 1976, Love 1978, Furness and Baillie 1981, Fowler et al. 1982). Nur et al. (1999a) estimated that the actual dispersal rate 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 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 Procellariiformes (Weimerskirch 1992, Pyle et al. 1997, Nur et al. 1999a). 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 petrel species.

We did not differentiate between males and females. 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.

References (Additional; Not in Main Section)

- 1444 Ainley, D. G., R. Podolsky, L. Deforest, G. Spencer, and N. Nur. 2001. The status and
1445 population trends of the Newell's shearwater on Kauai: insights from modeling. *Studies of*
1446 *Avian Biology* 22:108-123.
- 1447 Bradley, R. W., and P. Warzybok. 2003. Longevity record for ashy storm-petrel. *North*
1448 *American Bird Bander* 28:3.
- 1449 Fowler, J. A., J. D. Okill, and B. Marshall. 1982. A retrap analysis of storm petrels tape-
1450 lured in Shetland. *Ringin and Migration* 4:1-7.
- 1451 Furness, R. W., and S. R. Baillie. 1981. Factors affecting capture rate and biometrics of
1452 Storm Petrels on St Kilda. *Ringin and Migration* 3:137-148.
- 1453 Girman, D., W. J. Sydeman, and T. B. Smith. 1999. Population genetic structure of ashy
1454 storm-petrels. Chapter 2 in Nur, N., W. J. Sydeman, D. Girman, T. B. Smith, and D.
1455 Gilmer. 1999. Population status, prospects, and risks faced by two seabirds of the
1456 California Current: the ashy storm-petrel, *Oceanodroma homochroa*, and Xantus'
1457 Murrelet *Synthliboramphus hypoleucus*. Report to U.S. Geological Survey,
1458 Biological Resources Division.
- 1459 Huntington, C. E., R. G. Butler, and R. A. Mauck. 1996. Leach's Storm-Petrel
1460 (*Oceanodroma leucorhoa*). in *The Birds of North America*, No. 233 (A. Poole and F.
1461 Gill, Eds.). The Academy of Natural Sciences, Philadelphia, PA and the American
1462 Ornithologists Union, Washington, D.C.
- 1463 Love, J. A. 1978. Leach's and Storm Petrels on North Rona: 1971-1974. *Ringin and Migration*
1464 2:15-19.
- 1465 Mainwood, A. R. 1976. The movements of Storm Petrels as shown by ringin. *Ringin and*
1466 *Migration* 1:98-104.

- 1467 Mood, A. M., F. A. Graybill, and D. C. Boes. 1974. Introduction to the Theory of
1468 Statistics, 3rd Edition. McGraw-Hill, New York.
- 1469 Pyle, P., N. Nur, W J. Sydeman, and S. Emslie. 1997. Cost of reproduction and the
1470 evolution of deferred breeding in the Western Gull. Behavioral Ecology 8:140-147.
- 1471 Warzybok, P., R. Bradley, and S. N. G. Howell. 2009. First North American record of Tristram's
1472 Storm-Petrel (*Oceanodroma tristrami*). North American Birds 62(4):2-4.
- 1473 Weimerskirch, H. 1992. Reproductive effort in long-lived birds: age-specific patterns of
1474 condition, reproduction and survival in the wandering albatross. Oikos 64:464-73.
- 1475

1476

Appendix S3. Mouse Trapping Data

1477

Table S1. Mouse trapping success data. Results by month and year from Southeast

1478

Farallon Island, 2001-2004; 2010-2012.

Month/ Year	N, 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
Aug-02	22	84	0.262
Sep-02	112	168	0.667

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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

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Aug-11	78	96	0.813
Sep-11	89	99	0.899
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

1479

Appendix S4. Stochastic Simulation Results

Figure Legend.

Figure S1. Farallon ash storm-petrel simulation results illustrating stochastic variation in outcomes for the three trend scenarios (each with three owl reduction scenarios: 0%, 50%, and 80%) after 10 years (10,000 simulations for each trend x owl reduction combination). From top to bottom: 95th percentile outcome (green triangle), 75th percentile (red x), median (black filled circle), 25th percentile (red x), and 5th percentile (green triangle).

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