



Modeling the Impacts of House Mouse Eradication on Ashy Storm-Petrels on Southeast Farallon Island



Report to the U.S. Fish and Wildlife Service

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July 2013

Any reference to or use of this report or any portion thereof shall include the following citation:

Nur, N., R. Bradley, L. Salas, and J. Jahncke. 2013. Modeling the Impacts of House Mouse Eradication on Ashy Storm-Petrels on Southeast Farallon Island. Unpublished report to the US Fish and Wildlife Service. PRBO Conservation Science, Petaluma, California. PRBO Contribution Number 1880.

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Executive Summary

- This study provides quantitative estimates of the anticipated benefit to Ashy Storm-Petrels from proposed house mouse eradication on the South Farallon Islands.
- The objective of this study was to examine the ecological relationships between Farallon House Mouse abundance, Burrowing Owl abundance, Ashy Storm-Petrel predation by Burrowing Owls, and Ashy Storm-Petrel annual survival.
- Indices of House Mouse abundance, Burrowing Owl abundance, and Ashy Storm-Petrel predation by owls each showed a clear and distinctive seasonal pattern. Owls arrive at the island in the fall when mice are abundant. The owls then switch to preying upon storm-petrels after the mouse population crashes in December and January. There is a sharp peak observed in predation on Ashy Storm-Petrels by Burrowing Owls in February and March, during storm-petrel pre-breeding attendance.
- On a monthly basis, owl predation on storm-petrels is strongly positively related to Burrowing Owl abundance and strongly negatively related to House Mouse abundance, consistent with the view that mice are the primary prey and Ashy Storm-Petrels the secondary prey.
- Burrowing Owl abundance and predation on storm-petrels have increased in recent years, with especially high levels of both parameters in recent years. Annual variation in owl abundance and predation on storm-petrels are highly positively and significantly correlated.
- In assessing recent storm-petrel population index trends from 2000 to 2012, we evaluated twelve different models to determine the best parameterization describing the change in population index over time, as determined by AIC. The preferred model was a two part linear spline with a change point between 2006 and 2007. This break is consistent with the observed recent increase in Burrowing Owl numbers. Prior to the change point, the storm-petrel population index had increased significantly ($p < 0.001$). After the change point there was a significant change in trend ($p = 0.002$), resulting in a linear decrease in population ($p = 0.095$).
- As the best-fit negative linear population trend of 7.19% annual decrease (“Observed Steep Decline” scenario – Scenario A) was not statistically significant, we also assessed the sensitivity of our modeling results by considering two other scenarios: a “Moderate Decline” scenario – Scenario B - of 3.36% annual decline, and a “Near Stable” scenario – Scenario C - of 0.63% annual increase. We used these scenarios for modeling plausible future population trends.

- Capture-recapture analyses reveal a strong and significant effect of Burrowing Owl abundance on annual Ashy Storm-Petrel adult survival. Results of the survival analysis indicate that a 50% reduction in owl abundance can be expected to increase overall annual survival by 2.64 to 4.92%, depending on the scenario assessed.
- We estimate the change in population trend of Ashy Storm-Petrels as a result of anticipated reductions in Burrowing Owl predation on SEFI, using a population-dynamic model. A 50% reduction in Burrowing Owl abundance can be expected to change population growth rates by 2.3-3.9% depending on whether we assume Scenarios A or C, with Scenario B values in between. This corresponds to changing a population that is strongly declining to weakly declining (7.19% annual decline to 3.26%, Scenario A) or from near-stable to increasing (0.63% increase per year to 2.90% increase, Scenario C). Under Scenario B, population trajectory would change from declining at 3.36% per year to nearly stable at 0.22% decline per year. With a 71.5% reduction in the Burrowing Owl abundance index, population growth rates change by 3.1-5.3%, depending on the scenario. This greater reduction results in larger population benefits for storm-petrels (resulting in 1.88% annual decline under Scenario A and 3.69% annual increase under Scenario C).
- In summary, reduction in Burrowing Owl abundance has strong positive population impacts in all scenarios examined. Under Scenario A, the “Observed Steep Decline” scenario, rates of decline are substantially reduced, under Scenario B, the “Moderate Decline” scenario, the population trends change from moderate decline to stable or slight annual increase, and under Scenario C, the “Near Stable” scenario rates of annual population change from a very weak increase to a strong increase after owl reduction, a nearly five-fold increase in the net population growth rate.
- Reducing Burrowing Owl abundance, through elimination of their house mouse prey, will have a long term, substantial and significant effect in reducing overall Ashy Storm-Petrel mortality and promoting stable or increasing future population trends.

Introduction

Colonially breeding seabird populations worldwide face major threats, 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; they breed at an older age and have higher adult survival (Weimerskirch 2002). For extremely long lived, low-fecundity species such as those in the order Procellariiformes, the storm-petrels, shearwaters, and albatrosses etc. 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 one example where direct conservation action has had success is the elimination of introduced species impacting seabird colonies (review in Mulder et al. 2011).

Natural resource managers are primarily concerned with the often severe and obvious effects of predators on island-breeding seabird species, where the introduced predator decreases the abundance of prey species and can cause population declines (Schoener and Spiller 1996, Krajick et al. 2005). In addition, indirect interactions may exacerbate predation on prey species of concern. One example is hyper-predation, where there is an enhanced predation pressure on a secondary prey, due to either an increase in the abundance of a predator population that displays a numerical response to the primary prey, which itself may be an introduced species, or there is enhanced predation pressure due to a sudden decline in the abundance or availability of the primary prey (Howald et al. 2007). In both cases, with and without indirect effects, we have predation by a predator on a prey where the level of predation on the prey species of concern is determined by a third species. An example is Allen Cay Mice in the British Virgin Islands, which were recently eradicated as they were facilitating populations of Barn Owls to depredate Audubon's Shearwaters (Island Conservation 2012).

In this study, we analyze field data and develop statistical and population models to understand the inter-relationships among three species: an invasive rodent (House Mouse, *Mus musculus*), a native predator (Burrowing Owl, *Athene cunicularia*), and a seabird of conservation concern (Ashy Storm-Petrel, *Oceanodroma homochroa*) on Southeast Farallon Island, California (SEFI). In addition to examining variation in abundance among the three species over time, we also analyze field data on predation intensity by owls on the Ashy Storm-Petrel. Using a long-term mist-netting study of the

Ashy Storm-Petrel on SEFI (Bradley et al. 2011), we estimate the change in an index of adult survival with respect to variation in the abundance of Burrowing Owls. We then construct a population dynamic model that accounts for current population trends and estimate the change in future population trends that is expected given a reduction in owl predation activity.

The two primary objectives of this study are to:

1. Demonstrate the ecological relationships between House Mouse abundance, Burrowing Owl abundance, owl predation of Ashy Storm-Petrels, and Ashy Storm-Petrel annual survival.
2. Quantify the expected change in Ashy Storm-Petrel adult survival and consequent change in Ashy Storm-Petrel population trends as a result of anticipated reductions in Burrowing Owl predation on the South Farallon Islands.

Focal Species

House Mice

House mice are one of the most widespread invasive mammals on earth; amongst vertebrates the breadth of their global distribution is second only to that of humans (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 little conservation action devoted to mice on islands, relative to other introduced mammals (Wanless et al. 2007; Howald et al. 2007, Wanless et al. 2012). House mice were introduced to the South Farallon Islands sometime during the 1800's (Ainley and Boekelehide 1990). Despite over 40 years of continuous study of breeding seabirds on the Farallones, there is little evidence of direct effects of mice on breeding seabirds – though nest predation by mice is challenging to document. Mice on islands are known to directly depredate seabird eggs and chicks of several species (Mulder et al. 2011).

Burrowing Owls

The Burrowing Owl is found in the interior of California and other western States (Gervais et al. 2008). They arrive on the Farallones on their southbound fall migration (DeSante and Ainley 1980) starting in September. The arrival of migrating or dispersing landbirds onto the Farallones is not uncommon; over 400 different landbird species

have been recorded on the islands since 1968 (Richardson et al. 2003). Most landbirds that arrive on the Farallones depart within a few days (DeSante and Ainley 1980). However, Burrowing Owl arrival in fall occurs at the time the house mouse population is at its annual peak (Irwin 2006; also see Figure 2 - Results). Some Burrowing Owls now remain on the islands for up to several months, subsisting primarily on a diet of mice in the fall (Mills 2006; PRBO, unpubl. data). As we demonstrate in this study, in the winter months, the mouse population declines rapidly, severely reducing their availability as prey items for Burrowing Owl. Consequently, Burrowing Owl switch to alternative prey sources (Mills 2006; PRBO, unpubl. data). Adult storm-petrels, which begin to arrive on the islands starting in mid-winter to visit breeding sites and engage in courtship activity, and are nocturnal like the owls, become a major alternative prey item for the owls through the late winter and spring. Some owls die on the island during the winter (PRBO, unpubl. data). By May, all surviving Burrowing Owls have departed the island for their breeding grounds (this study). Burrowing Owls do not breed on the Farallon islands.

Ashy Storm-Petrel

The Ashy Storm-Petrel is a seabird species of major conservation concern. This small (~42 g), colonially breeding species is endemic to waters of the California Current, along the coast of California and Mexico (Spear & Ainley 2007), with breeding populations concentrated at the Farallon and Channel Islands (Carter et al. 2008). Sydeman et al. (1998a, 1998b) estimated a 44% decline in breeders, with a 95% confidence interval of 22-66% decline, in the population from 1972 to 1992 at Southeast Farallon Island (SEFI). The South Farallon Islands represents the largest colony for this species, with perhaps 50% of the world population (Carter et al. 2008). Due to major population declines, threats from colony predation, and at-sea mortality (e.g., from oil spills), the species has been listed as a California Species of Special Concern for many years (Carter et al. 2008) and was recently petitioned for listing under the Endangered Species Act. The Ashy Storm-Petrel is currently listed as “Endangered” by IUCN (2012) (<http://www.iucnredlist.org/apps/redlist/details/106003987/0>) due to its restricted geographic range, small population size, and apparent declines (Sydeman et al. 1998a, Ainley and Hyrenbach 2010).

The Ashy Storm-Petrel has been the subject of much study on the Farallon Islands (Ainley et al. 1990, Ainley 1995, Sydeman et al. 1998a). PRBO has conducted two

previous Population Viability Analyses (PVA), one that considered only the South Farallon Islands population (Sydeman et al. 1998b) and the second that expanded the geographic scope to include the Channel Islands population as well (Nur et al. 1999a). As part of the PVAs, Sydeman et al. (1998b) and Nur et al. (1999a) developed a population dynamic model that synthesized the best available demographic information on the Farallon population and accounted for observed population trends. Here we update the model developed by Nur et al. (1999a) based on the most recent observations and analysis of data since 1997. In particular, we analyze variation in annual survival of the Ashy Storm-Petrel, based on standardized mist netting that has been conducted continuously since 1992, with specific focus on estimating the effect of Burrowing Owl predation on Ashy Storm-Petrel survival during the period 2000 to 2012.

Methods

Field Data Collection

House Mice Abundance

House mice abundance was determined through monthly trapping success on 4 transect lines spread across island habitats (Irwin 2006). Trapping was conducted monthly for 3 nights between March 2001 to March 2004, and again from December 2010 to March 2012. Both sampling efforts used the same transects, each with 7 traps per transect. For the 2010-2012 effort 5 additional traps were added on a Lighthouse Hill transect. Trapping efforts used D-Con snap traps baited with peanut butter and oats. Trapping success was determined as the proportion of house mouse captures for the 84 (2001-2004) or 99 (2010-2012) traps set per monthly session.

Mistnetting of Ashy Storm-Petrels

Southeast Farallon Island is the largest of the 39 hectare South Farallon Islands, located approximately 48 km west of San Francisco, CA (Figure 1). As part of this study, we present an index of variation in population size based on statistical analysis of standardized mist-net captures. We use the population index to estimate change over time in the adult population of Ashy Storm-Petrels from 2000 to 2012.

We also estimate adult survival, specifically in relation to Burrowing Owl abundance (see “Statistical Analysis”) based on the same set of captured and recaptured Ashy Storm-Petrels. Survival analyses presented here are based on capture-mark-recapture

data of uniquely banded individuals. The survival analyses focus on 2000 to 2011 because of our focus on more recent years, and that the standardized Burrowing Owl abundance index was only available as of January 2000 (see below).

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. Two mist net sites were used (Lighthouse Hill [LHH] and Carpentry Shop [CS]; Figure 1) that 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. 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 a large amount of storm petrel breeding habitat and known high density of breeding sites (Sydeman et al. 1998a, PRBO 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 has 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 Ashy Storm-Petrel colony attendance (Ainley et al. 1990). Egg-laying by Ashy Storm-petrels typically commences in May (Ainley et al. 1990).

Social attraction, in the form of broadcast recordings of Ashy Storm-Petrel calls, was used during all net sessions to increase the chance of Ashy Storm-Petrel captures at the netting sites. A portable cassette tape player was placed at the base of the middle of the mist net and broadcast at a volume of ~65db throughout the netting sessions. The main calls on the tape were "flight calls," but in the background low frequency burrow "purring calls" and "rasping calls" are present (Ainley 1995). The flight call rate was approximately 0.44 calls per second or 26.5 calls per minute.

Ashy Storm-Petrel reproductive success

Ashy Storm-Petrel reproductive success (number of chicks fledged per pair) was determined for a sample of birds breeding in rock crevices in accessible habitat. In the absence of other data we assume similar reproductive success between accessible and inaccessible habitats, Clutch size for Ashy Storm-Petrel is 1 and birds can relay after failed breeding attempts (Ainley 1995). Beginning 5 May in each year, from 1992 to 2011, we checked all previously occupied breeding sites every 5 days to determine nest contents. All occupied sites were monitored for reproductive success, with a goal of at least 40 sites monitored each season. New sites were added annually during the breeding season by confirmed breeding of birds which responded to Ashy Storm-Petrel calls played during the day. Sites that had not been occupied for at least consecutive 5 years were dropped from further study. We used a flashlight and, starting in 2007, a small camera ("See Snake") to carefully and thoroughly examine each site. The camera allowed for increased sample size from 2007-2011, doubling the number of active sites we could follow. Once an egg was found or an adult was observed in incubation posture for two consecutive checks, the site was left undisturbed for 8 checks (40 days) before returning to check for hatch. Once a hatched chick was confirmed, the site was left undisturbed for an additional 8 checks. After the second skip period, we resumed checking the site every five days until the chick fledged. The "skip" periods help to reduce potential disturbance to incubating adults and young chicks. Chicks that were fully feathered and disappeared from their nesting crevice after 60 days of age were assumed to have fledged (Ainley et al. 1990). Reproductive Success was determined with respect to all attempts of a pair (including relays).

Ashy Storm-Petrel predation index

We developed an index of predation on Ashy Storm-Petrel from January 2003 to April 2012. Before 2003, data were not collected in a sufficiently systematic and standardized fashion. For each month beginning in 2003, we counted the number of depredated wings based on repeated, standardized surveys conducted every 5 days from March to August, supplemented by incidental collections throughout the year. Incidental collections were based on access to areas visited as part of long term studies at approximately the same time across all years. Thus, effort in September to February may not have been the same as in March to August but the effort was consistent from one year to the next. Identified remains were allocated to either Western Gull or

Burrowing Owl, 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 sharp contrast to storm-petrels consumed by Burrowing Owls, where wings are removed from the body before consumption and left unadulterated. Only remains positively identified as being caused by owls were used in this analysis. There is no evidence to suggest that predation rates on storm-petrels would differ in unsampled inaccessible areas.

Burrowing Owl abundance index

An index of Burrowing Owl abundance was determined based on daily observations of accessible areas from January 2000 to April 2012, as well as detailed roost surveys of Burrowing Owls conducted every 3 days from 2010 to 2012. As part of daily Farallon monitoring operations, island biologists searched the island for non-breeding birds and tally a total in the daily journal (Desante and Ainley 1980, Richardson et al. 2003). While effort varies through the year (i.e. ~8 hours in the fall and ~3 hours in the winter; owls are absent or rare May-August), effort is relatively consistent across years. However, to reduce effects of variation in daily sightings of owls, and allow for the fact that daily survey effort in earlier years was lower than in more recent years, we developed a robust and conservative index of Burrowing Owl abundance. The index was the maximum number of owls seen on a single day calculated for each month— as obtained by daily surveys throughout the time series and supplemented by roost surveys in recent years. Excluding May to August, when Burrowing Owl were absent or rare, the index varied from 1 to 10 in most months (mean = 2.85, SD = 2.78). During the four months from May to August each year, the monthly index was 0 (in 90% of the cases) or 1 (the other 10%).

A preliminary analysis indicated that the most consistent monthly metric of owl abundance was the maximum number of owls estimated to be on the island at any one time rather than mean or minimum per month; the maximum monthly value was more closely related to Ashy Storm-Petrel predation than were mean or minimum monthly values (see below).

For Ashy Storm-Petrel survival analyses, we examined several annual indices of Burrowing Owl abundance that differed with respect to which months were included. The most comprehensive measure was the mean of monthly maximum values

calculated for the months of September to April; Burrowing Owls were almost entirely absent during the months of May to August. The September - April measure showed a significant relationship with respect to Ashy Storm-Petrel survival (see below), and its effect was stronger than other Burrowing Owl abundance metrics (e.g., for January-April). In any case, all Burrowing Owl abundance metrics examined were highly correlated with each other and thus population modeling results presented here are not sensitive to which metric was chosen.

Statistical Analysis

Negative Binomial Regression Modeling for Population Index

We used negative binomial regression to analyze capture rates of Ashy Storm-Petrel in order to construct a population size index. Negative binomial regression allows for non-linear relationships and residuals that are not normally distributed, as was the case in this study. This method is especially suitable for count data, and is more suitable than Poisson regression as it accounts for over-dispersion. That is, the variance exceeds the mean, as is common in ecological studies (Carmen and Trivedi 1998; Hilbe 2007). Note that negative binomial regression models the natural logarithm $\ln(Y)$ in relation to a set of predictor variables, where, in this case Y = count variable; in other words, negative binomial regression uses a log-link function. No log-transformation is required prior to analysis; the analysis is carried out on Y with residuals assumed to be negative-binomially distributed.

We employed negative binomial regression (using program STATA 10.0) to model the dependent variable while controlling for variation in: hours of netting effort in a session, number of days spent netting at a site in a given year, Day of Year, $(\text{Day of Year})^2$, to allow for a quadratic seasonal effect, and site. In particular, we included "Year" as a categorical variable (i.e., as a factor) in order to derive year-specific estimates for the count variable, which was the goal of this analysis. The final full model included the two effort variables, the two date variables, site, and year as a categorical variable. This model was preferred by Akaike information criterion (AIC), used as a measure of goodness of fit, to models that had only a subset of these variables, i.e., the inclusion of each variable was justified with respect to AIC. This approach assumes that capture probability did not vary among years, other than that due to variation in the other predictor variables.

From the preferred model we estimated the year-specific effect for each year. The coefficient for the base year (2000) was set at 0.0, and the other coefficients were estimated as the difference in $\ln(\text{counts})$ for that year relative to the base-year (2000), after controlling for the other variables. For illustration purposes only, we graph the natural log values as the year-specific coefficient plus 1, in order to avoid negative values. For the purposes of analyzing trend, however, we analyzed the \ln -transformed values without addition of 1.

Analysis of Ashy Storm-Petrel Population Trends

To obtain a recent estimate of population change for use in the population model, we performed a set of regression analyses of \ln -transformed population index values (see above), comparing multiple models. In the simplest case, linear regression, the coefficient for a given time period, once back-transformed, estimates the constant proportional change for the specified time period (Nur et al. 1999b). Our prime objective was not to characterize historical change but to estimate population trend during the most recent period to then use in modeling the expected trajectory in the near future, during the period when mouse eradication is presumed to occur. We assessed 12 models to describe the previous 13 years of population \ln -based index values, including a constant, linear, quadratic, cubic, $\text{inverse}(\text{year})$, and $\ln(\text{year})$. We restricted our analyses to the period 2000-2012, with 2012 the most recent year for which we had data. We did not model population trends before 2000 for two reasons: 1) oceanographic conditions in the 1990's were much different from that experienced in the period 2000-2012 (Peterson and Schwing 2003, Doney et al. 2012), and so of questionable relevance for future projections, and 2) mouse, owl abundance and owl-predation data were not available prior to 2000.

In addition to the six models listed above, we also assessed 6 models of linear splines to determine whether an apparent change in trend occurred, from linear increasing to linear decreasing trend, during the period between 2005 and 2008. We chose this period as the wide data range where a possible change in trend may have occurred, after initial data examination (see Results). The 6 models examined assessed all possible change points in that period, with the change point occurring in a given year, or the change occurring between 2 years. We tested change points at 2005, 2006 and 2007; and half-way between 2005 and

2006, 2006 and 2007, and 2007 and 2008. AIC values were used to determine the best fit model. We then used the best fit model to model the trajectory for the most recent period, in this case a negative linear trend from 2007 to 2012, with the change in trend occurring between 2006 and 2007 (see Results). As presented below, the best estimated trend for 2007 to 2012 was that of a steep decline.

However, because of considerable uncertainty around the estimated trend value, we assessed sensitivity of our analyses to the assumption of this “Observed Steep Decline” trend, described subsequently as Scenario A. We considered two alternatives to Scenario A: first, a moderate decline equal to the estimated slope coefficient plus 1 standard error (i.e., a decline of about one-half the magnitude of the observed decline) - Scenario B - and second a “near stable” scenario – Scenario C, in which the trend was equal to the observed coefficient plus 2 standard errors. In other words, we examined **three scenarios** with regard to future population trajectory: A) a steep decline (results of the best-supported population trend model for the period 2000-2012), B) a moderate decline, and C) a near-stable, slightly increasing trend.

Calculation of an Ashy-Storm Petrel Population Estimate

We estimated the current Farallon Ashy Storm-Petrel population size from the negative binomial regression analysis of mist-netting using year-specific estimates for each of the 3 most recent years, 2010, 2011, and 2012. Results from 3 most recent years is, in our view, more robust than relying on results from a single year. We determined the weighted 3-year mean (calculated in natural log values) and then backtransformed it. Weighting was based on the inverse of the standard error of the annual estimate (Kutner et al. 2004). To estimate the current number of breeders on SEFI, we used the estimated proportional change from 1992 to 2010-2012 and multiplied that by 2660, the number of breeders estimated by Sydeman et al. (1998b). All breeder estimates are rounded to the closest even number of individuals.

To obtain a 95% Confidence Interval (CI) around this 3-year estimate of proportional population change, we followed several steps. First, we calculated the mean annual standard error from the standard errors around the annual, year-specific coefficients obtained from the negative binomial regression analysis

using output from 2010-2012. Second, we obtained the “3-year mean SE” by dividing the mean annual SE by the square-root of n , where n = number of years used to obtain the mean standard error, i.e., $n = 3$. Third, we constructed an approximate 95% CI as estimated population change (in ln-units) plus or minus 2 times the “3-year mean SE.” The upper and lower CI bounds were then backtransformed to obtain upper and lower estimates of proportional change.

Statistical Estimation of Effects of Burrowing Owls on Survival of Ashy Storm-Petrels

We used the package RMARK (Laake et al. 2012) to analyze Ashy Storm-Petrel capture-recapture data and thus estimate survival and recapture probabilities and effects of covariates on these. Our goal was to obtain reliable estimates of survival probability, not to estimate recapture probability. However, in order to obtain the former, we needed to obtain reliable estimates of recapture probability (Cooch et al. 1996). We constructed a capture history table that included all Ashy Storm-Petrels captured between years 2000 and 2012, maximizing overlap between our Ashy Storm-Petrel mistnetting and Burrowing Owl abundance datasets. The following covariates of survival were included in the set of competing models we evaluated: Burrowing Owl abundance index (described elsewhere in this Report), capture site (LHH vs. CS), Southern Oscillation Index values in winter (SOI), and all possible combinations of these three variables. To model recapture probabilities, we considered the following covariates: site, effort (net hours per year), SOI, and all combinations of these three variables. We also modeled year-specific variation in survival (with year as a factor, not as a continuous covariate), but for the population modeling component of this study we were concerned only with estimates reflecting specific covariates, especially Burrowing Owl abundance.

The SOI influence on Ashy Storm-Petrel survival was included in our survival models because January-March SOI has been shown previously to predict Cassin’s Auklet (*Ptychoramphus aleuticus*) adult survival on the Farallones (Lee et al. 2007, Nur et al. 2011). We therefore expected Ashy Storm-Petrel may also respond to the biophysical effects associated with winter SOI. We included SOI in the recapture models because we wanted to ascertain the influence of SOI on the behavior of the birds. For example, it is possible that, under some large-scale climatic conditions, birds may be more likely or less likely to attempt to breed on the Farallones in a given year, thus influencing their

chances of re-capture. SOI values from <http://www.cgd.ucar.edu/cas/catalog/climind/SOI.signal.ascii> were obtained on a monthly basis. We summarized the SOI values from two intervals that we suspected may best reflect the influence of the large-scale climatic conditions on Ashy Storm-Petrel survival and recapture in the Farallones: the period from December to February and the period from January to March, both prior to the initiation of egg-laying. In a preliminary analysis, the latter period's SOI showed a stronger effect on survival and recapture probabilities, so we used it in our final models.

We included capture site in the estimation of recapture probability because there may be differences in the capture probabilities for these two sites, which differ in a number of respects (see above). Differences between sites may be reflected in the composition of transients vs. true resident birds. Transient birds have low fidelity to the vicinity of the trapping location; they are non-breeders and thus are unlikely to be recaptured in subsequent years (Nur et al. 1993). If transients are more common at one site compared to the other site, this will be reflected in differences in site-specific capture probabilities. Any method that can improve our estimate of recapture probability will also improve our ability to estimate survival. However, our goal in the capture-recapture analysis was not to estimate absolute survival probability but rather the relative difference in survival probability, especially in relation to differences in Burrowing Owl abundance. For this reason, we included site in modeling recapture probability and survival probability (Cooch et al. 1996).

Burrowing Owl abundance was estimated by averaging "maximum owls per month" over a specified period of months. We considered several different time periods, but the two time periods that were both statistically predictive and ecologically meaningful were: (1) September to April, the 8 months during which Burrowing Owls are on the island and (2) just January to April. The justification for considering the latter is that owl predation on Ashy Storm-Petrels is almost entirely confined to these four months (see Figure 2 below). We evaluated a total of 128 models: First, we ran 64 models with various combinations of 0 to 3 covariates for survival (site, Burrowing Owl abundance, SOI) and 0 to 3 covariates for recapture probability (site, netting hours, SOI), for which the Burrowing Owl abundance metric was the September to April mean monthly value. Second, we ran another set of 64 models in which the Burrowing Owl abundance metric was the January to April metric instead of September to April. We chose the top model among the 128 examined, i.e., the one that optimized AIC, and use these results for

inclusion in the predictive population dynamic model. Specifically, the statistical model results were used to indicate the change in logit survival with a change in Burrowing Owl abundance (logit survival is the dependent variable used in capture-recapture analyses; Cooch et al. 1996). The change in logit survival was converted into a change in absolute survival and this was used in the population model; note that:

$$\text{logit survival} = \ln[(\text{survival probability})/(1-\text{survival probability})].$$

Population Modeling of Ashy Storm-Petrels

Overview and Approach Used

To assess and quantify the impact of a change in Burrowing Owl abundance and predation on Ashy Storm-Petrel, we developed a deterministic population dynamic model for the Farallon Island population, building on previous modeling by Nur et al. (1999a) for this same population.

Our modeling approach was to first construct a population dynamic model that could best account for recent, observed Ashy Storm-Petrel population trends on SEFI, given field observations, previous studies, and the scientific literature. The estimation of recent population trend (during the period 2000-2012) is described in this report. However, to allow for uncertainty regarding estimates of recent trend and therefore uncertainty about population trends in the near future, we consider three scenarios that span a range of plausible trends, based on our statistical analysis of the mistnetting index: A) steep decline, B) moderate decline, and C) near-stable. For each trend scenario, we developed a population-dynamic model that reproduced the presumed trend. To do so, we derived three different estimates of baseline (current) survival in the absence of mouse eradication (described below), one for each population-trend model.

We then incorporated changes in adult survival associated with presumed changes in Burrowing Owl abundance on the Farallon Islands with respect to these three trend scenarios. These presumed changes in Burrowing Owl abundance in turn reflect the likely consequences of proposed mouse eradication. The next step was to model the population dynamics of Ashy Storm-Petrels, given the presumed, statistically estimated, changes in survival resulting from reduction in Burrowing Owl predation, considering the three possible baseline (pre-eradication) trend scenarios.

The changes in adult survival were directly estimated from the statistical analysis of the 13-year dataset (capture histories from 2000 to 2012) during which time we had independent estimates of Burrowing Owl abundance on a monthly and annual basis.

Thus, the pre-eradication parameter values used were derived from population dynamic models that reflects scenarios consistent with recently observed population trends; the postulated post-eradication parameter values reflect, in addition, our statistical analysis of the effect of Burrowing Owls on Ashy Storm-Petrel population dynamics.

Parameters of the “Current Population Dynamic Model”

There are six important demographic processes that a seabird population dynamic model needs to incorporate (Nur & Sydeman 1999). The first two concern survival, the next three are components of reproductive success, and the sixth is the balance between emigration and immigration. We discuss each in turn.

- 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%. We did not use this value, but instead adjusted survival values of adults to produce three trend scenarios: (A) a population that exhibited the same population trajectory as has recently been observed (a decline of approximately 7.2% per year, see “Results”), (B) a moderate decline (of approximately 3.4% per year) and (C) a near-stable population (increase of approximately 0.6% per year).
- ii) **Survival of juveniles and subadults.** We followed Nur et al. (1999a), who in turn followed 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. By the fourth year of life, Ashy Storm-Petrels have begun breeding, and so we assumed that survival in their fourth year reached adult levels.
- 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 elsewhere in this report. For the population modeling, we used the mean reproductive success observed for this population over the last 10 years (2002-2011).

- 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, assuming they have survived. We believe this assumption is valid 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 relied on a field study of the closely related Leach's Storm-Petrel (*O. leucorhoa*). 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. This does not mean that, for example, 100% of seven year olds bred, but rather that by age 7, Ashy Storm-Petrel breeding probability reached 100% of the adult value for breeding, 92% (see above). Thus, our model assumes that most Ashy 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, USGS unpublished, PRBO 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* – PRBO unpublished), but which then return to their natal colonies when they reach maturity (Nur & Sydeman 1999). Wide ranging behavior of immature storm petrels of multiple 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%, which is still a low rate of immigration. In the population dynamic model we allow for some immigration and emigration but assume that immigration equals emigration; that is, 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 would be affected.

Additional assumptions

We assumed no maximum longevity. Ashy 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 (beyond prime breeding age) displayed slightly lower adult survival rates, consistent with other studies of seabirds (Pyle et al. 1997, Nur et al. 1999a). Model results were robust to the assumption of maximum age because few adults are expected to survive beyond age 36.

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.

Starting Population Size

As this analyses focused on changes in trends, we depicted population modeling results, with and without impacts of mouse eradication, by setting relative population size in Year 0 to 1.0. Year 0 corresponds to the year in which Burrowing Owl abundance is reduced, presumably a result of mouse eradication. Thus, for example, a change in relative population size from 1.0 in Year 0 to 0.5 in Year 20 indicates a 50% decline. Sydeman et al. (1998b) estimated a breeding population on the Farallon Islands of 2,660 in 1992; Nur et al. (1999a) estimated that the total population size in 1992 (including subadults and non-breeders) was a little less than 5,000 individuals.

We estimated the current Farallon Ashy Storm-Petrel population size from the negative binomial regression analysis of mist-netting using year-specific estimates for each of the 3 most recent years, 2010, 2011, and 2012. Results from 3 most recent years are, in our view, more robust than relying on results

from a single year We determined the weighted 3-year mean (calculated in natural log values) and then backtransformed it. Weighting was based on the inverse of the standard error of the annual estimate (Kutner et al. 2004). To estimate the current number of breeders on SEFI, we used the estimated proportional change from 1992 to 2010-2012 and multiplied that by 2660, the number of breeders estimated by Sydeman et al. (1998b). All breeder estimates are rounded to the closest even number of individuals.

To obtain a 95% Confidence Interval (CI) around this 3-year estimate of proportional population change, we followed several steps. First, we calculated the mean annual standard error from the standard errors around the annual, year-specific coefficients obtained from the negative binomial regression analysis using output from 2010-2012. Second, we obtained the “3-year mean SE” by dividing the mean annual SE by the square-root of n , where n = number of years used to obtain the mean standard error, i.e., $n = 3$. Third, we constructed an approximate 95% CI as estimated population change (in ln-units) plus or minus 2 times the “3-year mean SE.” The upper and lower CI bounds were then backtransformed to obtain upper and lower estimates of proportional change.

Population model Leslie matrix: population size and calibration

Population projections were carried out using an age-based Leslie matrix as described above. The elements of the Leslie matrix were held constant over time. Reproductive success was based on recent (10-year) observations in the field (see above for details). Assumptions regarding survival and breeding probability are described above. For each scenario we calculated the adult survival rate that, with the other parameter values set (described above), produced a population whose finite growth rate was either 7.19% decline per year (Scenario A), 3.36% decline per year (Scenario B), or 0.63% increase per year (Scenario C), as described in the Results. Note that adjustment of adult survival also resulted in proportional adjustment of survival rates of first-year, second-year and third-year individuals, as described above. As noted, fourth-year individuals were presumed to display adult survival values.

Population model: modeling impacts of Burrowing Owl predation

The result of the calibration process was that the population dynamic model produced a population that displayed one of three trends over time, corresponding to the three scenarios: Scenario A) steep decline, Scenario B) moderate decline, and Scenario C) near-stable. These correspond to population behavior observed in recent years, under conditions in which Burrowing Owl abundance and predation activity has been high.

Thus, we used the “recent population dynamic model” to represent three plausible baseline condition scenarios: the expected population trends in the near future if there were no change in abundance of Burrowing Owl on the island. The “baseline-recent” model, with its three scenarios, is one in which we extrapolate into the future and assume that current conditions continue for the next 20 years - presumably with both mice and owls present.

The next stage of modeling was to estimate the change in the storm-petrel population trend resulting from a change in survival, as a result of an assumed reduction in Burrowing Owl abundance and predation on the island. The change in storm-petrel survival rates was determined from the statistical analysis of mist-net capture-recapture data.

We analyzed the most recent 3 years of data(2009/2010 to 2011/2012) on Burrowing Owl abundance on SEFI to provide the most relevant values regarding current owl levels and how these may be changed in the future as a result of mouse eradication. We considered 2 levels of Burrowing Owl abundance reduction for modeling purposes: reducing abundance by 50% and 71.5% compared to the mean observed for the 3 most recent years. The mean value for the last three years for maximum number of Burrowing Owls observed per month over the 8-month observation period, September to April (see above) was 6.29. The 50% scenario corresponds to a reduction of 3.145 “owls” and the 71.5% scenario corresponds to a reduction of 4.50 “owls,” as measured by the mean value of the index, which is the maximum number of Burrowing Owls observed per month.

We suspect that migrating Burrowing Owls may still land on the Farallon Islands in the fall in the future even if all house mice are eradicated. But it is likely that they will move on with their migration within a few days to a few weeks, when no adequate available food source is present. Thus, while it is reasonable to expect that most burrowing owl predation on storm-petrels can be reduced with mouse eradication, it may not result in 100% reduction in Burrowing Owl predation on storm-petrels. For owls arriving in

September and October, as many do, there will still be limited opportunities to prey upon Ashy Storm-Petrels, but the storm-petrels available as prey are present in relatively low numbers during those months, compared to their peak abundances. If 100% reduction of Burrowing Owl predation could be accomplished, the population response of Ashy Storm-Petrels would be even greater than what we have modeled.

Furthermore to model the benefit to Ashy Storm-Petrels of a reduction in Burrowing Owl predation, we assumed that first-year and second-year storm-petrel survival did not improve as a result of Burrowing Owl reduction, but only survival of third-year and older individuals improved. For the purposes of modeling, we assumed that second-year birds were absent from the island, but that third-year birds were present and that they are susceptible to predation just as are older individuals. Whereas we have good reason to believe that fourth-year birds are present on the island, we have little information as to whether second- and third-year individuals are present (and therefore subject to Burrowing Owl predation) or absent. Our mist-net data for storm petrels contains very few birds banded as chicks, and so most capture birds are of unknown age. The assumption made in our modeling was intermediate between two more extreme assumptions (complete susceptibility of second- and third-year individuals vs no susceptibility of second and third-year birds).

In summary, we model three levels of reduction in Burrowing Owl abundance: a) No owl reduction, b) 50% owl reduction and c) 71.5% owl reduction. These three levels are each assessed for three different scenarios of population trend: the observed recent steep decline, a moderate decline, and a near stable scenario. For each scenario we consider a 20-year time horizon.

Results

Monthly variation

House mice, Burrowing Owl abundance, and Ashy Storm-Petrel predation by owls each showed a clear and distinctive seasonal pattern (Figure 2). For mice, the population index was lowest in March-May and highest in August-December. For owls, the abundance index was high in October-March and near zero in June-August. The index of owl predation on Ashy Storm-Petrel was highest in February-April, and near zero in June-December. Thus, two temporal trends can be noted: 1) the Ashy Storm-Petrel predation index increases in January and February, just as the house mouse index drops precipitously; 2) at the time that

Burrowing Owls arrive on the island (in September and October), house mouse populations are at very high levels. Despite presence of owls in September and October, months that coincide with peak house mouse levels, predation on Ashy Storm-Petrel is near zero at this time, even though a number of Ashy Storm-Petrels are still breeding in those months (Ainley et al. 1990). This pattern is consistent with mice being the preferred prey of Burrowing Owls.

Most of the monthly variation in the Ashy Storm-Petrel predation index (ln-transformed) was explained by variation in Burrowing Owl abundance and the house mouse abundance index ($R^2 = 0.538$; Adj $R^2 = 0.502$; $P < 0.0001$, Table 1). The effect of Burrowing Owl abundance on owl predation of storm-petrels was highly significant when controlling for the abundance of mice: greater monthly owl abundance was associated with greater predation on Ashy Storm-Petrel ($P = 0.001$; Table 1). The effect of house mouse abundance was highly significant when controlling for the effect of Burrowing Owl abundance ($P < 0.001$; Table 1). Greater house mouse monthly abundance was associated with lower Burrowing Owl predation index values for Ashy Storm-Petrel. This finding also suggests that when mice are available, Ashy Storm-Petrels are not the primary prey for Burrowing Owls.

Annual Variation in Population Size and Predation

Annual Trends in Burrowing Owl abundance and Ashy Storm-Petrel predation

Burrowing Owl abundance appeared relatively stable from fall 2000 to 2006 and then began to increase (Figure 3). The overall trend depicted is significant ($P = 0.001$); the best fit, as determined by AIC was a quadratic transformation, i.e., an accelerating increase over time beginning in 2000, the first year of the time-series (Figure 3). Note that the four years of highest abundance have been the four most recent years (2009-2012).

The results of the analysis show that Burrowing Owl predation on Ashy Storm-Petrels has also increased during the same period (Figure 4). Like the Burrowing Owl abundance index, the trend in the owl predation index on petrels is both significant and accelerating ($P = 0.003$). The best fit, as determined by AIC is the

quadratic transformation of year relative to 2003, the first year of standardized data collection for this variable.

Furthermore, the annual Ashy Storm-Petrel owl predation index is strongly, positively correlated with the annual index of Burrowing Owl abundance. The linear relationship between the two is highly significant ($P = 0.003$; $R^2 = 0.740$; $R^2_{adj} = 0.703$). This result strongly suggests that the recent increase in the Burrowing Owl abundance has led to an increase in predation on Ashy Storm-Petrels.

Variation in Index of Ashy Storm-Petrel Population Size

The Ashy Storm-Petrel population index displayed marked year-to-year variation from 2000 to 2012 (Figure 5). In assessing recent storm-petrel population index trends from 2000 to 2012, we evaluated twelve different models to determine the best parameterization describing the change in population index over time, as determined by AIC. The preferred model was a two part linear spline with a change point between 2006 and 2007 (Table 2, Figure 5). This break, or “knot,” is consistent with the observed increase in Burrowing Owl numbers (Figure 4; see above). Prior to the change point, the storm-petrel population index had increased significantly at 22.1% per year ($p < 0.001$, Table 3). After the change point there was a significant change in trend ($p = 0.002$, Table 3) with a linear decrease in population ($p = 0.095$, Table 3). The trend for the period 2007-2012 was equivalent to a 7.19% decrease per year, which we refer to as the “observed steep decline” scenario. However the standard error around the trend estimate was large, hence the 95% CI included zero. Because the negative trend of 7.19% annual decrease for the period 2007 to 2012 was not statistically significant and its CI was quite large (Table 3), we also considered two other plausible scenarios based on our empirical estimates. It is likely that the 6 year timeframe is too short to produce a significant result with these methods, despite the strong decline. One alternative scenario was a “moderate decline” which was equal to the estimated slope plus 1 standard error, i.e., 3.36% decline per year. The second alternative was equal to the estimated slope plus 2 standard errors, i.e., 0.63% increase per year. We refer to the three scenarios as Scenarios A (“observed steep decline”), B (“moderate decline”) and C (“near-stable”). Population models were calibrated to yield Leslie matrices whose population growth rates corresponded to one of these three scenarios (Table 4). The

calibration was achieved by adjusting adult survival (see Methods); demographic parameter values are shown in Table 4.

Ashy Storm-Petrel Population Estimate

Using estimates from the three year period 2010-2012, the estimated change in Farallon Ashy Storm-Petrel was 2.17x as many breeders during this period as in 1992. We estimate 5768 breeders ($= 2660 \times 2.1681$), a 116.8% increase from 1992 to 2010-2012.

The lower bound estimate of population size obtained was a proportional increase of 42.4%; the upper bound estimate was a proportional increase of 230.0%. This translates into lower and upper bounds of the 95% CI of 3790 breeders and 8778 breeders respectively.

Variation in Ashy Storm-Petrel Survival Probability

There was support for year-to-year variation in survival (Likelihood Ratio Statistic = 16.51; $df = 10$, $P = 0.086$), comparing a model with year as a factor with a model with constant survival. Of greater relevance was the dependence of annual survival on Burrowing Owl abundance. Specifically, the optimal model (among 128 examined) included two variables affecting survival: Sept-April index of Burrowing Owl abundance and location of mist-netting site (LHH vs. CS). The preferred model also included two variables affecting recapture probability: site and winter SOI. The coefficients and other statistics for the preferred model are depicted in Table 5.

The most relevant result for the modeling is that an increase in the Burrowing Owl index by 1 individual (per month, over the 8-month period) decreased logit survival by 0.1131. The effect is highly significant ($P = 0.009$, Table 5). Therefore a reduction in the Burrowing Owl index by 50% is expected to increase logit survival by 0.356 for the 3 scenarios examined. A reduction in the Burrowing Owl index by 71.5% is expected to increase logit survival by 0.509.

Note that all three scenarios (A, B, and C) assume the same change in logit survival as a function of a change in the Burrowing Owl index, as enumerated above. However, baseline survival rates differ for the three scenarios and thus the change in survival

associated with a change in the Burrowing Owl index differs among the scenarios (Table 6). The estimated magnitude of the effect of reducing (or increasing) Burrowing Owl abundance was large: a decrease of 1 Burrowing Owl in the abundance index (= 8 “owl-months”, based on known numbers of owls) is associated with an absolute increase in survival of 0.8% to 1.4%, depending on the baseline value of survival. Specifically, a 50% reduction in Burrowing Owl abundance during the 8 month period, as calculated for the past 3 years (equivalent to a reduction in the Burrowing Owl abundance index of 3.145 owls, based on known numbers of owls), is expected to increase adult storm-petrel survival by a relative 2.64 to 4.92% for adults, depending on the scenario; a 71.5% reduction in Burrowing Owl abundance (equal to reduction in the index of 4.5 owls, based on known numbers of owls) is expected to increase adult storm-petrel survival by a relative 3.54 to 6.66% for adults, depending on the scenario (Table 6).

Population Dynamic Model

We developed a population dynamic model for Ashy Storm-Petrels that produced a population that declines at 7.19%, declines at 3.36%, or increases at 0.63% per year, depending on the scenario examined. The demographic parameter values for each scenario are listed and annotated in Table 4. Adult survival varied from 84.3% to 91.4% depending on the scenario. We then modified survival of all individuals beyond second-year individuals (see Methods) under the two “Burrowing Owl reduction levels”, for scenarios A, B, and C. Adult survival values predicted as a result of a decrease in the Burrowing Owl index are depicted in Table 6. The new lambda values under the two Burrowing Owl reduction levels for the three population trend scenarios are also depicted in Table 6. Changes in relative Ashy Storm-Petrel population size over a twenty year time period, for all three levels of Burrowing Owl reduction (0%, 50% and 71.5% reduction) for each population trend scenario are displayed in Figure 6.

The most important results to emerge from this analysis are: A 50% reduction in Burrowing Owl abundance can be expected to change population growth rates by 2.3-3.9% depending on whether we assume Scenarios A or C, with Scenario B values falling in between. This corresponds to changing a population which is declining at 7.2% per year to one that is declining at only 3.3% per year (under Scenario A) or will change a population that is slightly increasing (at 0.6% per year) to one that is increasing at

2.9% per year (under Scenario C). Again, under Scenario B, results are intermediate: the model predicts a change from 3.4% decline to near-stability (0.2% decline per year).

With a 71.5% reduction in the Burrowing Owl abundance index, population growth rates change by 3.1-5.3%, depending on the scenario. The greater reduction in Burrowing Owl abundance (and therefore predation) results in larger population benefits for storm-petrels: the result is a much more modest decline (1.9% per year compared to 7.2% decline with no Burrowing Owl reduction) under Scenario A or a much stronger increase (3.7% per year compared to 0.6% increase per year) under Scenario C. Under Scenario B, we see a modest increase (0.9% per year) instead of a 3.4% decrease per year.

In summary, reduction in Burrowing Owl abundance has strong positive Ashy Storm-Petrel population impacts in all scenarios examined. Under the “Observed Steep Decline” scenario, rates of storm-petrel decline are drastically reduced, under the “Moderate Decline” scenario the storm-petrel population trends change from moderate decline to stable or slight annual increase, and under the “Near Stable” scenario, rates of annual storm-petrel population change from a very weak increase to a strong increase with owl reduction, equivalent to a five-fold increase in the net population growth rate.

Discussion

Our statistical analysis demonstrates that observed variation in Burrowing Owl abundance and predation on Ashy Storm-Petrel do indeed result in ecologically and statistically significant changes in Ashy Storm-Petrel survival. Given these impacts, we can expect, all else being equal, that a decrease in Burrowing Owl abundance will have significant and positive benefits for Ashy Storm-Petrel population trends. Our results show that even a 50% reduction in Burrowing Owl abundance resulting from a proposed invasive rodent removal can be expected to change a steep decline to a moderate decline, change a moderate decline to near-stability, or change a relatively stable population to a growing population. A reduction of recent Burrowing Owl abundance by substantially over 50% has the potential to produce increasing Ashy Storm-Petrel populations on SEFI in two out of the three population trend scenarios assessed. These results provide quantitative evidence supporting the expected benefits to the Ashy

Storm-Petrel population from the proposed house mouse eradication on the Farallones, which would provide a significant conservation gain for this species endemic to the California Current. The benefit is especially marked since the South Farallon Islands are home to approximately half of the world's Ashy-Storm Petrel population.

The monthly data presented here indicate that Ashy Storm-Petrels are a secondary prey item for Burrowing Owls. Burrowing Owls appear to prefer house mice as prey, and depredate Ashy Storm-Petrels when mice are not available. Both the monthly and annual data demonstrate that more Burrowing Owls on SEFI results in greater predation on Ashy Storm-Petrel by owls. Most importantly, the Ashy Storm-Petrel survival analysis indicates that, on an annual basis, more Burrowing Owls present results in lower adult Ashy Storm-Petrel survival. The estimated effect of a reduction in Burrowing Owl abundance was large: A reduction of Burrowing Owl abundance by 16% relative to current levels (equal to 1 Burrowing Owl in the monthly abundance index), is expected to increase Ashy Storm-Petrel survival by approximately 1%. A 50% reduction in owl abundance is expected to increase survival probability by 0.024 to 0.042. This is quite significant for the population because current adult mortality, from all causes, is in the range of 0.086 to 0.156. For a long-lived seabird, such reductions in mortality and increases in survival rates are of great consequence in improving population viability (Weimerskirch et al. 2002)

Our measure of predator abundance or activity is coarse, but provides an index of year to year variation in attendance of Burrowing Owl on SEFI, an open terrain where owls have persistent, identifiable roost sites. We acknowledge that daily survey effort increased in 2010, so we have used the monthly maximum Burrowing Owl abundance observed on SEFI. The monthly index integrates observations over many days and therefore is less sensitive to the effort in any given day. Moreover, the high correlation ($r = 0.860$) observed between the annual index of Burrowing Owl abundance and the annual index of Ashy Storm-Petrel predation by owls, an index whose methods have been consistent throughout the time series, provides strong evidence of a causal relationship between Burrowing Owl abundance on SEFI and variation in mortality rates of Ashy Storm-Petrel. In fact, analysis of the Ashy Storm-Petrel predation index in relation to annual survival yields very similar results as those presented here with respect to impact of changes in Burrowing Owl abundance.

In addition, the timing of the recently observed increase in Burrowing Owl abundance, which began in 2007 (Figure 3), aligns with the change point from an increasing

population to a declining population in the top model selected to describe recent population trends. That is, during the period 2001 to 2006, Burrowing Owl abundance remained stable and low, during which time the Ashy Storm-Petrel population was growing. Starting in 2007, Burrowing Owl abundance began to increase, and the population trend changed from positive to negative. These are all lines of evidence that support our finding of a statistically significant effect of Burrowing Owl abundance on Ashy Storm-Petrel survival as revealed through the capture-recapture analyses.

The recent increase in Burrowing Owl abundance at SEFI may be due to population increases in Burrowing Owls, or changes in the coastal distribution of this primarily inland species, though there are no published studies to support these hypotheses. As there is no long term time quantitative series on SEFI mouse abundance, it is possible that changes in their numbers have influenced owls, though mice have always been abundant on SEFI in the fall for the last 4 decades (PRBO, unpublished data). The most recent four years have seen the greatest abundance values for Burrowing Owl, and so the current levels of this predator present a grave problem for Ashy Storm-Petrel, if no action is taken.

It is rare in ecological studies to have direct evidence of variation in predation rates that are so tightly coupled with observations on the predator itself (variation in Burrowing Owl abundance) as well as the demographic parameter of interest (variation in survival rates of Ashy Storm-Petrel). Thus, we believe the quantitative relationship between owl abundance and Ashy Storm-Petrel survival rates elucidated here is well-supported. The longer current levels of owl predation continue, the more likely this population is to decline. It should also be noted that these analyses do not include effects of Western Gull predation on Ashy Storm-Petrel, whose overall, population-level impact is similar to that of owl predation. However, per individual, the predation rates of Burrowing Owls on Ashy Storm-Petrels is 775 times that of Western Gulls (Bradley et al. 2011). To reduce the Western Gull predation levels on Ashy Storm-Petrels by a substantial amount, a very large number of Western Gulls would likely need to be removed from the island. Reducing gull predation would have positive impacts for Ashy Storm-Petrel populations, but reduction of Western Gull predation is not required for the population to switch from decline to stability or from stability to growth: a large reduction in Burrowing Owl predation will suffice.

In summary, there is strong evidence for current, significant impacts of Burrowing Owl predation on Ashy Storm-Petrel population dynamics. To what extent mouse

eradication results in reduction of Burrowing Owl predation on storm-petrels remains to be seen, but indications from this study and other island eradications indicate that there will likely be a positive and significant population response by Ashy Storm-Petrels and other native species to the removal of the invasive rodent from the Refuge. Eradication of house mice may not prevent migrating Burrowing Owls from visiting the Farallon Islands in the fall. However, it is likely that the owls would leave soon after arriving, as mice would not be present and the few chick rearing storm-petrels that are still present make direct flights to and from their breeding sites, not the extensive flight activity they show during courtship and pre-breeding, where they would be more susceptible to owl predation (PRBO, unpublished). Thus, owls would likely not stay several months on the island, as they currently do, preying on Ashy Storm-Petrels in January through April. In particular, there are few or no Ashy Storm-Petrels on the Farallon Islands in November and December (Ainley et al. 1990, PRBO unpublished). It is not plausible, from an energetic point of view, that Burrowing Owls would continue to stay on the island during those months in the absence of both their primary prey (house mice) and their secondary prey (Ashy Storm-Petrel). Predation on other seabirds by Burrowing Owls has rarely been observed (PRBO, unpublished).

Caveats and Limitations

We have used analyses of capture rates of Ashy Storm-Petrels to provide an index of population change. Our analyses have controlled for several variables that may influence capture probability (days of netting, hours of netting, date, the quadratic effect of date, and capture location) but there may indeed be annual differences in capture probability not accounted for by our statistical model. In fact, the survival analysis identified SOI as a factor that may explain annual variation in recapture probability. We emphasize; however, that we have used the population index results to inform us regarding longer-term changes in the abundance of Ashy Storm-Petrels, not year to year changes. We use the change-point analysis of mistnet capture rates in two ways. First, the change-point analysis demonstrated a significant difference between population trend in 2000 to 2006 and the trend from 2007 to 2012. We have no reason to infer that this change in trend was due to a change in capture probability, but this possibility cannot be ruled out. Instead, we argue that the change in trend is consistent with the change in survival rates associated with the marked increase in Burrowing Owl abundance and increase in the predation index, that began about 2007. Comparing 2000-2006 with 2007-2012, Burrowing Owl abundance was about four-fold higher in the

recent period, and the predation index was more than twice as great. However, we are certainly not arguing that this was the only factor explaining the change in trend.

Second, we have used the change-point analysis to characterize the recent population trend, a decrease of 7.2% per year. There is substantial uncertainty around this estimate and therefore in our analyses we have considered three possible current trends, from a very slight increase (less than 1% per year) to a steep decline (over 7% per year). Our results do not depend on assuming any one trend estimate. Though the quantitative results depend on which scenario is assumed, the qualitative results are the same: a 50% reduction in Burrowing Owl abundance is expected to change the annual population growth rate by 2 to 4% per year; a 71.5% reduction in Burrowing Owl abundance is expected to change population growth rate by 3 to 5% per year.

While we produced a recent population estimate for Farallon Ashy-Storm Petrels based on index values from mist-net captures, this analysis focused on changes in trends not absolute numbers. Due to the cryptic nature of this species, it is extremely difficult to estimating breeding population size and the sampled area (and likely resulting estimate) did not include all portions of the islands. The large confidence interval around this population estimate reflects these challenges.

We did not consider direct impacts of house mice or Burrowing Owl on Ashy Storm-Petrel reproductive success (see Wanless et al. 2012). Reproductive success of storm-petrels may increase as a result of house mouse eradication, either directly or indirectly. The direct effect would be a possible reduction in egg and chick mortality due to house mice eradication – though evidence of direct mice effects on breeding Farallon storm petrels is minimal (Ainley et al. 1990, PRBO, unpublished). Indirect effects would result from decreases in Ashy Storm-Petrel parental mortality before or during the egg stage (in March and April) due to reduction in Burrowing Owls at this time, resulting in increased breeding attempts and/or increased breeding success.

It is also important to note that our analyses on abundance of owls and their predation on storm-petrels are using index values collected from accessible areas of the island, and over 40% of island area at the South Farallones (particularly West End Island) is not surveyed, therefore absolute values for owl abundance and predation of storm-petrels are higher than index values.

Our projections do not specifically incorporate impacts of environmental variability on future population trends, in contrast to analyses by Nur et al. (2011) and Nur et al.

(2012). The goal of our analysis was to determine the impacts to Ashy storm-petrels as a result of a change in predation rates by Burrow Owls. In the variable marine environment of the California Current, reduction of predation impacts will help Ashy Storm-Petrel populations buffer potentially poor oceanic conditions in the future.

Acknowledgments

We thank all of the Farallon biologists who supervised these studies, and all of the volunteer field assistants who helped collect the data. We thank the US Fish and Wildlife Service for permission to work on the Farallon National Wildlife Refuge. We also thank the Farallon Patrol for their support with transportation to the Farallones. Funding was provided by the Packard Foundation. We thank Gerry McChesney, Brian Halstead, and Holly Gellerman for their comments on this report. This is PRBO contribution # 1880.

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Table 1. Regression Analysis of Ashy Storm-Petrel Predation index (ln-transformed), by month, in relation to House Mouse and Burrowing Owl monthly indices.

Number of observations = 29. Test of overall model: $F(2,26) = 15.12$; $P < 0.0001$. $R^2 = 0.538$, $R^2_{\text{adj.}} = 0.502$

Variable	Coefficient	S.E.	t	P value
House Mouse trapping index	-3.463	0.674	-4.96	$P < 0.0001$
Burrowing Owl abundance index	+0.199	0.056	+3.55	$P = 0.001$
Intercept	+1.745	0.301	+5.80	$P < 0.0001$

Table 2. Model results of Farallon Ashy Storm Petrel Population Index (ln-transformed) trends 2000-2012, ranked by AIC values. k = number of model parameters. For linear spline models, the change point is shown; 2006/2007 indicates change point is half-way between 2006 and 2007, etc.

Model	k	AIC
Two Part linear spline : 2006/2007	3	0.110
Two Part linear spline : 2005/2006	3	0.183
Two Part linear spline : 2007	3	0.193
Two Part linear spline : 2005	3	0.338
Two Part linear spline : 2006	3	0.784
Quadratic	3	0.827
Two Part linear spline : 2007/2008	3	1.256
Cubic	4	2.755
Ln (year)	2	5.873
Inverse year	2	7.543
Linear	2	11.052
Constant	1	17.075

Table 3. Regression Analysis of best fit model Farallon Ashy Storm-Petrel Population Index (ln-transformed) trends 2000-2012: two part linear spline with the change point between 2006 and 2007. Comparing overall trends before and after the change point show significant change in overall trend: $F(1,10) = 17.06$, $P = 0.002$.

Number of observations = 13. Test of overall model: $F(2,10) = 20.08$; $P = 0.0003$. $R^2 = 0.801$, $R^2_{\text{adj.}} = 0.761$

Variable	Coefficient	S.E.	P value	Lower 95% CI	Upper 95% CI
Index prior	+0.200	0.034	$P < 0.001$	0.125	0.275
Index post	-0.075	0.040	$P = 0.095$	-0.165	0.016
Intercept	-399.588	67.311	$P < 0.001$	-549.567	-249.609

Table 4. Ashy Storm-Petrel Demographic Parameter Values Used to Model Current Conditions with no Burrowing Owl Reduction. Three different scenarios are modeled: A) “Observed Steep Decline”; B) “Moderate Decline”; and C) “Near Stable”

Age	Proportional Survival to Mature Adult ¹	Steep Decline Survival ²	Moderate Decline Survival ²	Near-Stable Survival ²	Breeding Probability ³	Breeding Success ⁴
1	0.72	0.607	0.632	0.658	0	0
2	0.86	0.725	0.755	0.786	0	0
3	0.98	0.826	0.860	0.896	0	0
4	1	0.843	0.878	0.914	0.092	0.588
5	1	0.843	0.878	0.914	0.460	0.588
6	1	0.843	0.878	0.914	0.828	0.588
7	1	0.843	0.878	0.914	0.920	0.588
8	1	0.843	0.878	0.914	0.920	0.588
9	1	0.843	0.878	0.914	0.920	0.588
10	1	0.843	0.878	0.914	0.920	0.588
11	1	0.843	0.878	0.914	0.920	0.588
12	1	0.843	0.878	0.914	0.920	0.588
13	1	0.843	0.878	0.914	0.920	0.588
14	1	0.843	0.878	0.914	0.920	0.588
15	1	0.843	0.878	0.914	0.920	0.588
16+	0.98	0.826	0.861	0.896	0.920	0.588

¹ - From Nur et al.1999a

² - Adult survival calibrated to produce population lambda for relevant scenario

³ - Fraction of individuals of that age class that attempt to breed, either for the first time or as an experienced breeder.

⁴ - Mean value, SEFI, 2002-2011

Table 5. Ashy Storm-Petrel Survival Estimation Results for Top Model, 2000-2011 for Southeast Farallon Island. For the model, Survival (Φ) is a function of site and Sept-April Burrowing Owl abundance; recapture probability (p) is a function of site and Jan-Mar SOI. Model statistics: Number of parameters = 6, $-2\ln\text{Likelihood} = 2635.107$, $\text{AICc} = 2647.124$.

Parameter	Estimate	St. Error	Lower 95%CI	Upper 95%CI
Phi: Intercept	1.398	0.281	0.847	1.950
Phi: site (LHH vs CS)	-0.997	0.283	-1.552	-0.443
Phi: Burrowing Owl abundance	-0.1131	0.0413	-0.1941	-0.0321
p: Intercept	-3.740	0.202	-4.136	-3.345
p: site (LHH vs CS)	0.973	0.245	0.494	1.452
p: SOI	0.050	0.030	-0.009	0.110

Likelihood ratio test for effect of Burrowing Owl (compared to corresponding model without Burrowing Owl index): $\text{LRS} = 6.743$, $\text{df} = 1$, $P = 0.009$.

Table 6. Impact of a Change in Burrowing Owl Abundance on Southeast Farallon Island on Ashy Storm-Petrel Populations. These results are based on Burrowing Owl and Ashy Storm-Petrel data from 2000-2012. Three different scenarios are: A) with the modeled recent decline; B) the recent decline plus one standard error; and C) the recent decline plus two standard errors, the upper boundary of the 95% confidence interval for our modeled results of recent population trends. A decrease of 3.145 in the Burrowing Owl Index corresponds to a reduction of 50% in Burrowing Owl abundance over recent years (2010-2012). A decrease of 4.5 in the Burrowing Owl Index corresponds to a reduction of 71.5% in Burrowing Owl abundance over recent years (2009-2012), and the value observed in 2011/2012.

A: “Observed Steep Decline” Scenario

Change in Burrowing Owl Index	Adult Survival	Change in Survival	Percent Change in Survival	Lambda	Change in Lambda	Population Growth Rate	Description
0	0.8434	0	0%	0.9281	0	7.19% decline	Recent trend, no change in Burrowing Owl
Decrease by 3.145	0.8849	0.0415	4.92%	0.9673	0.0392	3.27% decline	Recent trend; decrease by 50% of recent mean
Decrease by 4.5	0.8996	0.0562	6.66%	0.9812	0.0531	1.88% decline	Recent trend; decrease by 72% of recent mean

B: “Moderate Decline” Scenario

Change in Burrowing Owl Index	Adult Survival	Change in Survival	Percent Change in Survival	Lambda	Change in Lambda	Population Growth Rate	Description
0	0.878	0	0%	0.9664	0	3.36% decline	Trend +1 SE, no change in Burrowing Owl
Decrease by 3.145	0.9113	0.0333	4.02%	0.9978	0.0314	0.22% decline	Trend +1 SE; decrease by 50% of recent mean

Decrease by 4.5	0.9229	0.0449	5.11%	1.0088	0.0424	0.88% increase	Trend +1 SE; decrease by 72% of recent mean
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C: "Near Stable"

Change in Burrowing Owl Index	Adult Survival	Change in Survival	Percent Change in Survival	Lambda	Change in Lambda	Population Growth Rate	Description
0	0.9142	0	0%	1.0063	0	0.63% increase	Trend +2 SE, no change in Burrowing Owl
Decrease by 3.145	0.9383	0.0241	2.64%	1.029	0.0227	2.90% increase	Trend +2 SE; decrease by 50% of recent mean
Decrease by 4.5	0.9466	0.0324	3.54%	1.0369	0.0306	3.69% increase	Trend +2 SE; decrease by 72% of recent mean

Figure 1. Ashy Storm-Petrel netting sites on Southeast Farallon Island, CA. The two mist-netting locations are shown. Inset depicts general location of the Farallon Islands.

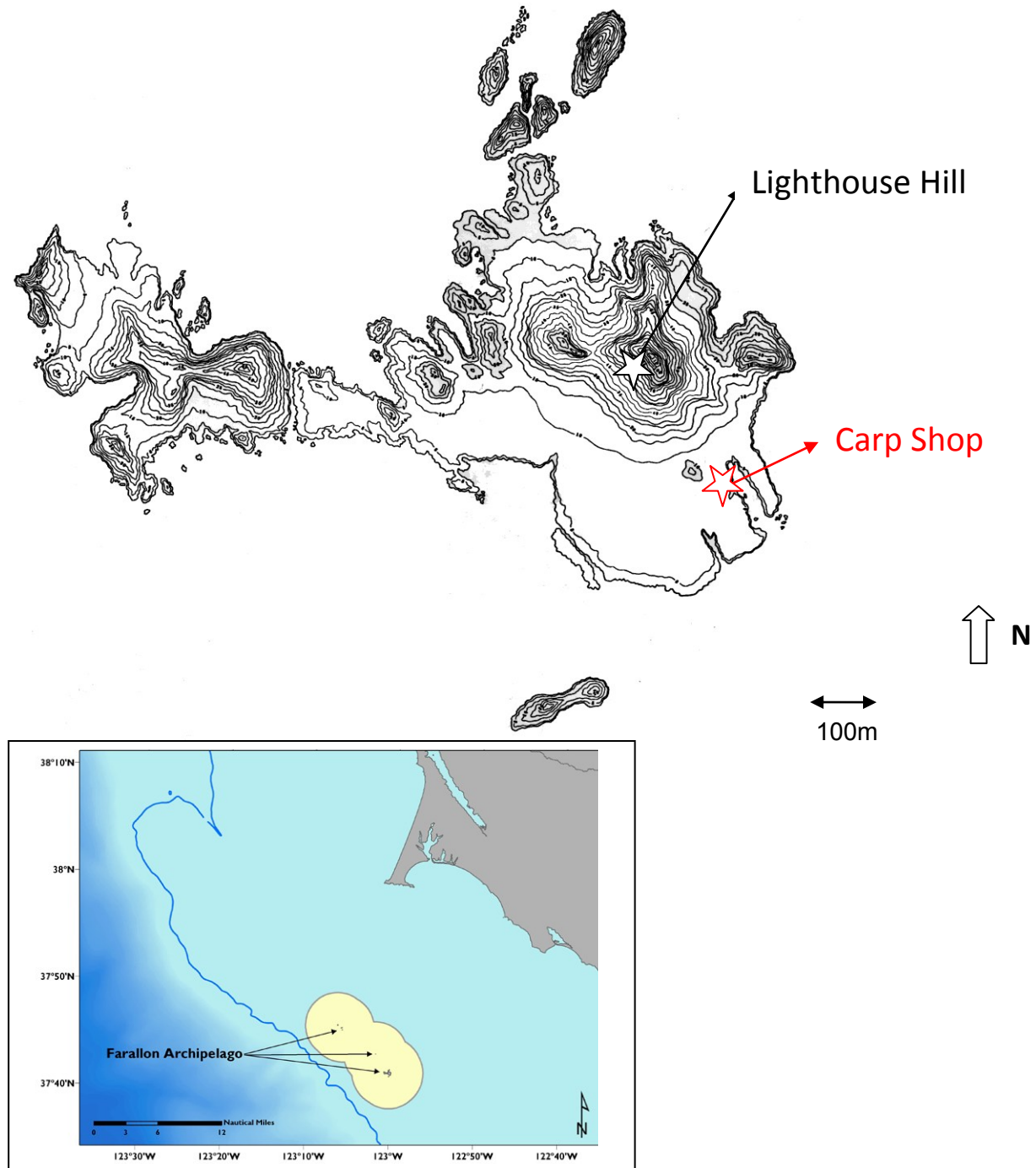


Figure 2. Seasonal Cycle of House Mouse Abundance Index (2001-2004, 2011-2012), Index of Ashy Storm-Petrel predation by Burrowing Owl (2008-2012), and Burrowing Owl abundance Index (2008-2012) at Southeast Farallon Island. Monthly mean values with standard deviation are shown.

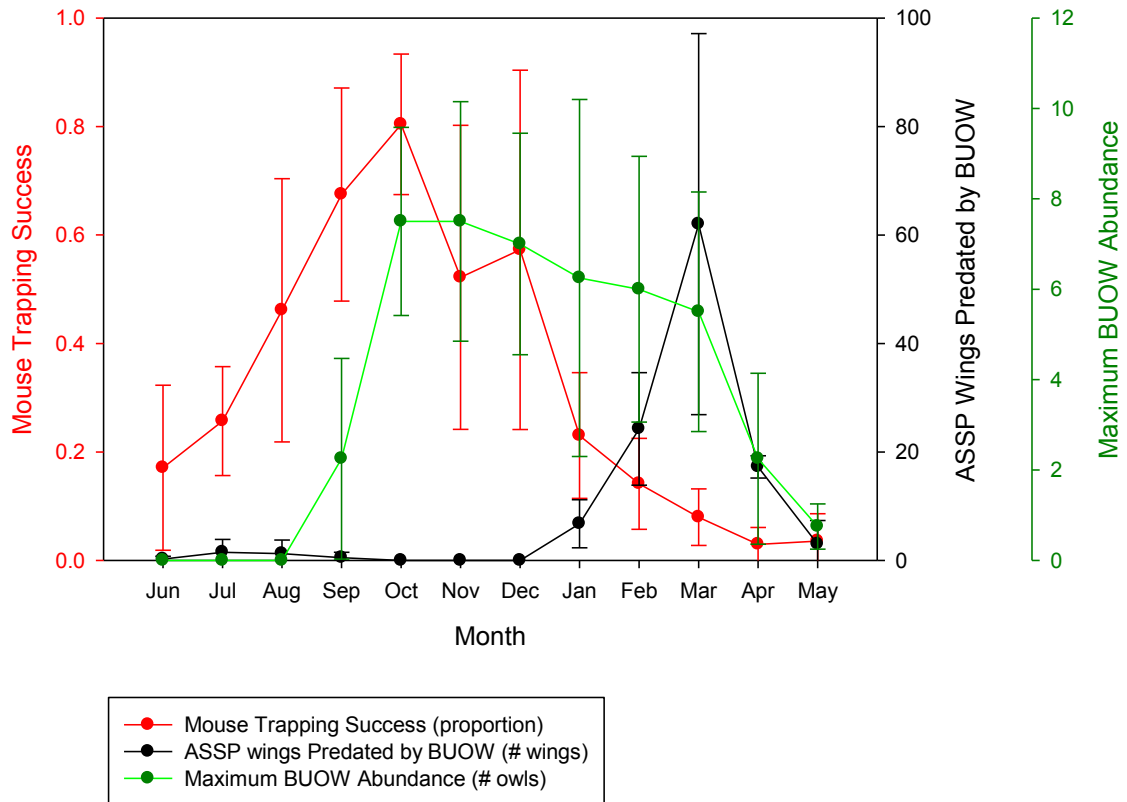


Figure 3. Variation in the annual Burrowing Owl abundance index (mean Sept-April abundance) for 2001 to 2012 on Southeast Farallon Island. The curve of best fit, as determined by AIC, is shown: a quadratic, accelerating trend. $P = 0.001$

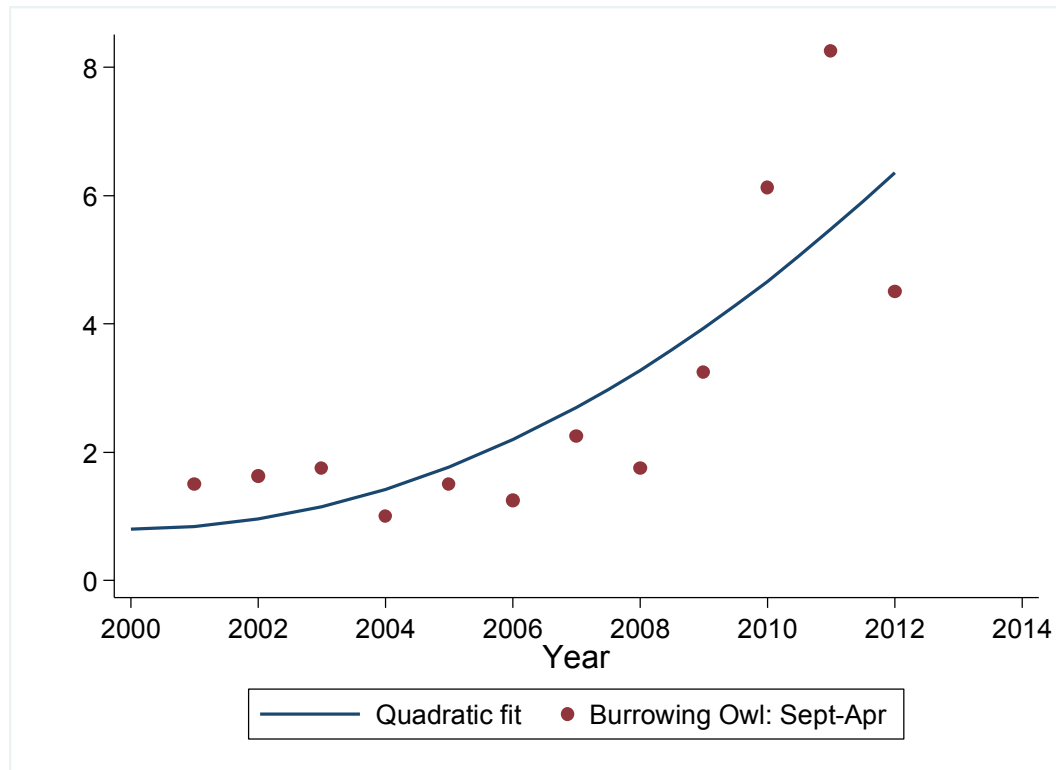


Figure 4. Annual (January-December) index of Burrowing Owl predation on Ashy Storm-Petrels from 2003 through 2011 on Southeast Farallon Island. 2012 data is not included in this figure, as only data through April was available at the time of analysis. The curve of best fit, as determined by AIC, is shown: a quadratic, accelerating trend. $P=0.003$

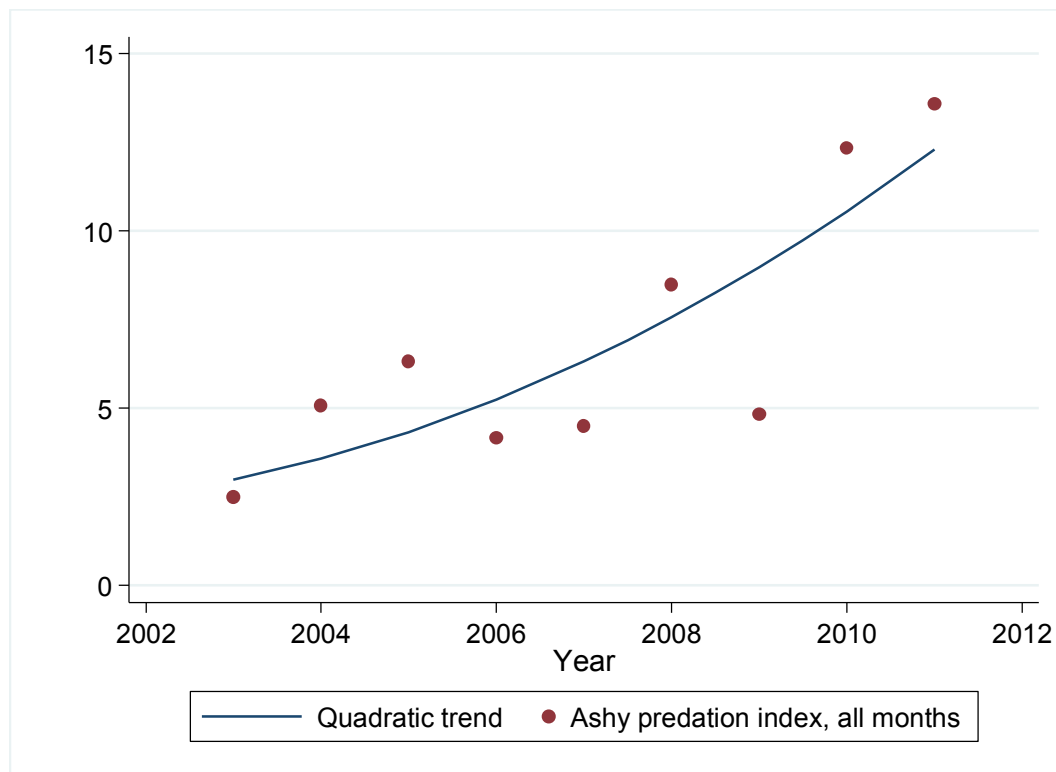


Figure 5. Population Index from Mist-netting Analyses for Ashy Storm-Petrels, 2000 to 2012 from Southeast Farallon Island. Values shown are natural log of the population index, plus one. The index is set at 1 for 2000 for illustrative purposes, though analyses were conducted with 2000 value set to 0 (see Methods). Index values are presumed directly proportional to abundance of Ashy Storm-Petrels. Line is best fit change point analysis showing change in linear trend between 2006 and 2007. Slopes in the two time periods were significantly different ($t=4.13$, $df=10$, $p=0.002$; Table 3)

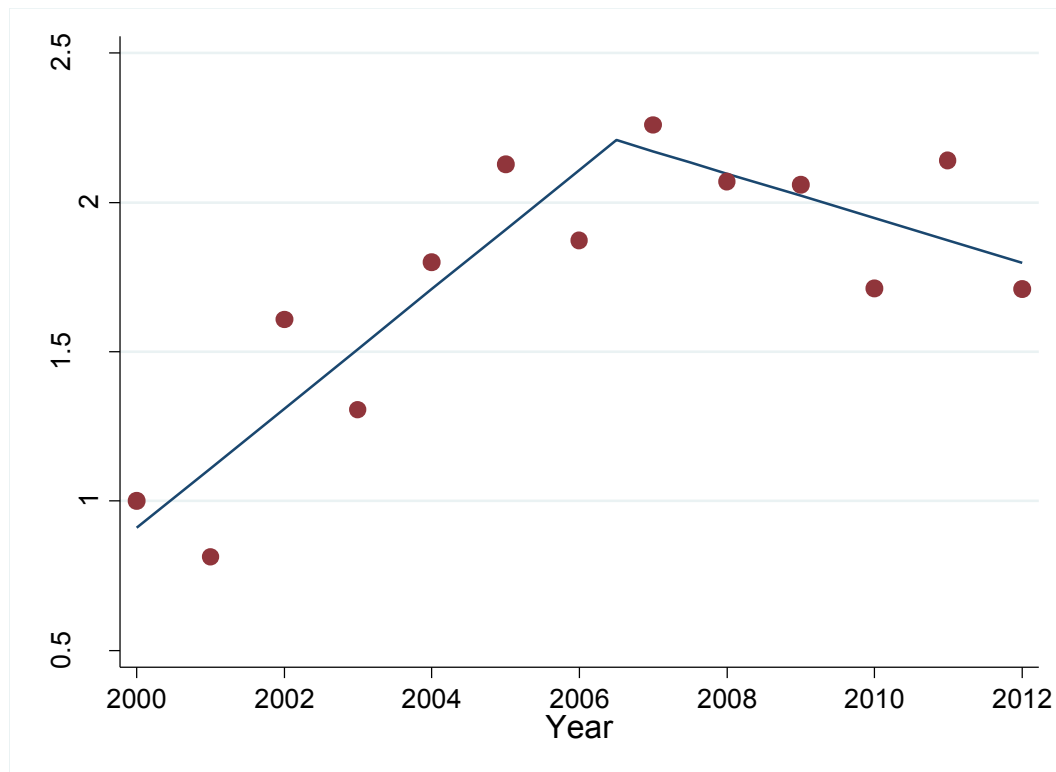
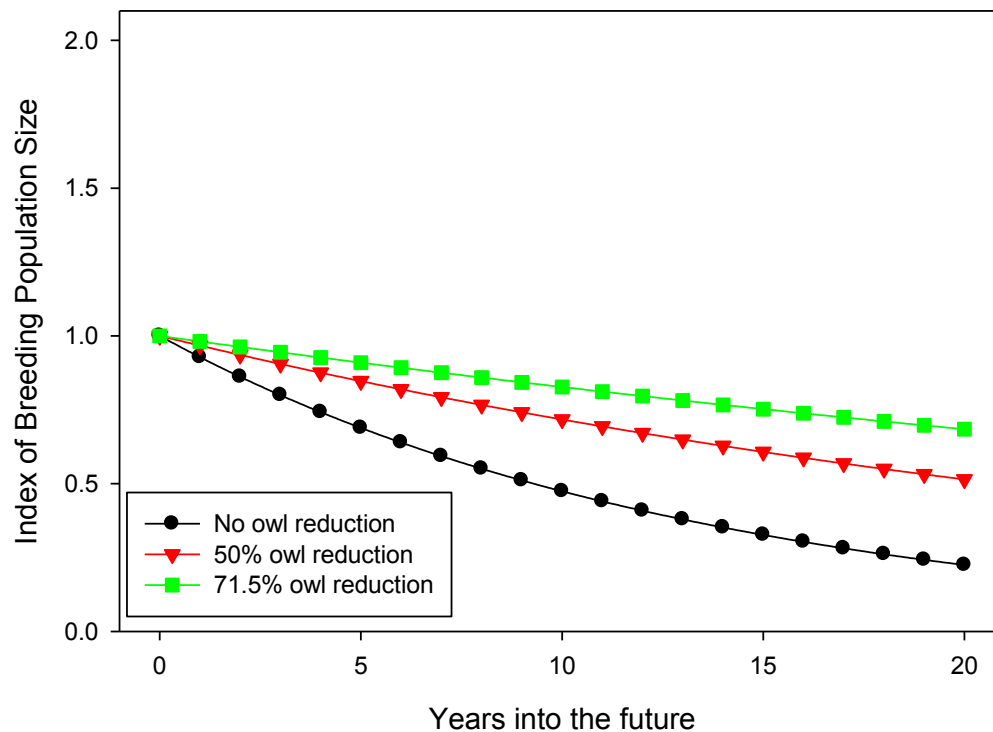
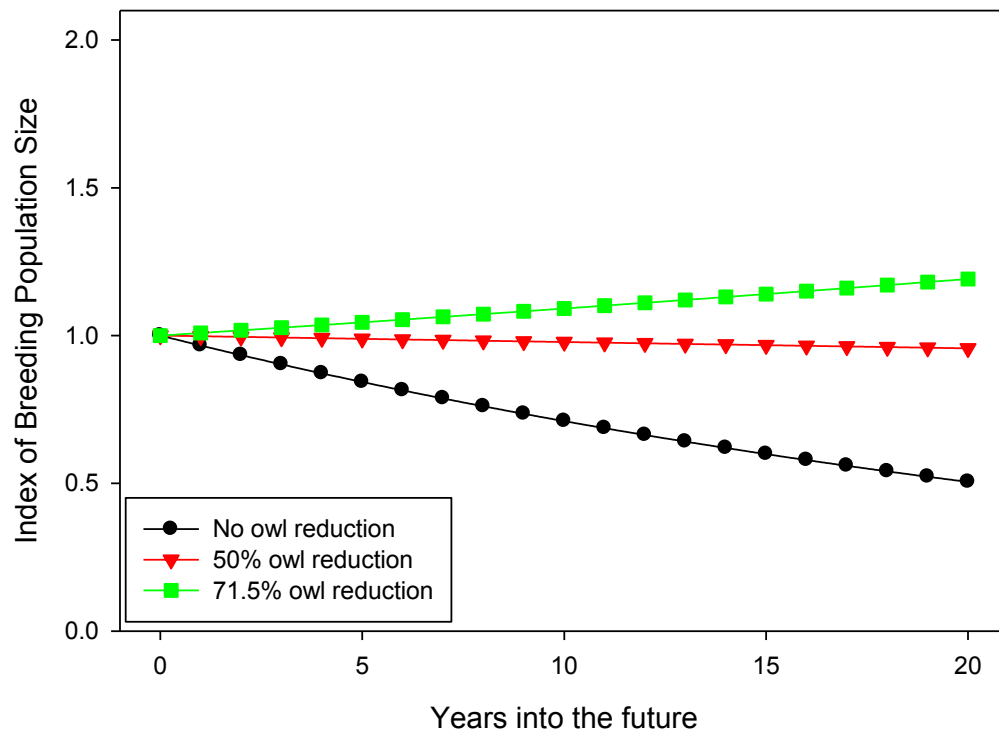


Figure 6. Farallon Ashy Storm-Petrel Population projections under the three levels of reduction in Burrowing Owl Abundance: 0% reduction, 50% reduction, and 71.5% reduction (see Methods). Levels of reduction are modeled for three separate scenarios: A) “Observed Steep Decline”; B) “Moderate Decline” ; and C) “Near Stable” (see Methods). Depicted are relative breeding population sizes for a 20-year period with Year 0 set to 1.0. Year 0 corresponds to most recent conditions and it is during this year that Burrowing Owl reduction is initiated, hence the population is assumed to respond between Year 0 and Year 1.

A) “Observed Steep Decline” Scenario



B) “Moderate Decline” Scenario

C) “Near Stable” Scenario