



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



Report to the U.S. Fish and Wildlife Service

Nadav Nur, Russell Bradley, Leo Salas, and Jaime Jahncke

PRBO Conservation Science
3820 Cypress Drive #11
Petaluma, CA, 94954

October 2012

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. 2012. Modeling the Impacts of House Mouse Eradication on Southeast Farallon Island. Unpublished report to the US Fish and Wildlife Service. PRBO Conservation Science, Petaluma, California. PRBO Contribution Number 1880.

For further information contact the director of the California Current at marinedirector@prbo.org or PRBO Conservation Science, 3820 Cypress Drive #11,

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, reflecting the fact 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.
- Capture-recapture analyses reveal a strong and significant effect of Burrowing Owl abundance on annual Ashy Storm-Petrel adult survival. A 50% reduction in owl abundance can be expected to reduce overall annual mortality by 27%.
- 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. With no reduction in Burrowing Owl abundance (assuming recent conditions continue into the future) the storm-petrel population is expected to decrease by 27.4% over a 10 year period.
- A 50% reduction in Burrowing Owl abundance can be expected to change a declining storm-petrel population into one that is approximately stable: increasing by 0.7% after 10 years. With a 71.5% reduction in the Burrowing Owl abundance index, an increasing population is expected, increasing by 11.8% after 10 years.
- 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 trait 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. But 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 predate Audubon's Shearwaters (Island Conservation 2012).

In this study, we analyze field data explaining the inter-relationships among three species: an invasive rodent (House Mouse, *Mus musculus*), an introduced 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. We argue that the available evidence indicates that removing the invasive house mice will eliminate or substantially reduce Burrowing Owl predation on Ashy Storm-Petrels. This study provides quantitative estimates of the benefit to Ashy Storm-Petrels from the proposed invasive house mouse eradication.

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 Boekehide 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 these interactions would be difficult to document. Mice on islands are known to directly predate on 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 at first (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. 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, and become a major alternative prey item for the owls through the late winter and spring. Some owls die on the island during the winter. By May, all surviving Burrowing Owls have departed the island for their breeding grounds. Burrowing Owls do not breed on the 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). This 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 (<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 (1999) 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. (1999) 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 abundance on Ashy Storm-Petrel survival during the period 2000 to 2011.

Methods

Field Data Collection

Mistnetting of Ashy Storm-Petrels

Southeast Farallon Island is the largest of the 39 hectare South Farallon Islands, located approximately 35 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-Petrel from 1992 to 2011.

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 focused on 2000 to 2011 because standardized Burrowing Owl abundance 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) and 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 1992-2011, 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.

Field Methods: 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. 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 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. Reproductive Success was determined with respect to all attempts (including relays).

Ashy Storm-Petrel predation index

We developed an index of predation on Ashy Storm-Petrel for the years 2003 to 2011. 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 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. We used data from January 2003 through April 2012. Identified remains were allocated to either Western Gull or Burrowing Owl, or were classified as unknown predator. Only remains positively identified as being caused by owls were used in this analysis.

Burrowing Owl abundance index

An index of Burrowing Owl abundance was determined based on daily observations from January 2000 to April 2012, as well as detailed roost surveys of Burrowing Owls every 3 days from 2010 to 2012. As part of daily Farallon

monitoring operations, island biologists search 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), 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; this metric (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., January-April). In any case, all Burrowing Owl abundance metrics examined were highly correlated 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 variance exceeds the mean, as is common in ecological studies (Carmen and Trivedi 1998; Hilbe 2007). Note that negative binomial regression analyzes the natural logarithm $\ln(Y)$ in relation to a set of predictor variables, where, in this case Y = count variable. No log-transformation is required for the analysis; the analysis is carried out on Y .

We employed negative binomial regression (using program STATA 10.0) to model the dependent variable, $\ln(\text{counts})$, 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 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), 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.

From the preferred model we estimated the year-specific effect for each year. The coefficient for the first year in the time series (1992) 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 (1992), after controlling for the other variables. We then back-transformed the year-coefficient values, since the negative binomial coefficients were on a natural-log scale. The back-transformation provided an index value of 1.0 for 1992 (i.e., $e^0 = 1.0$); the values for all other years were then the proportional change in each year relative to the base-year. For example, a value of 1.65 for year X indicated that counts were 65% higher in that year compared to 1992, once the other variables were controlled for. We use these index values as our measure of changes in relative population size.

Analysis of Ashy Storm-Petrel Population Trends

To obtain a recent estimate of population change for use in the population model, we performed a regression of \ln -transformed population index values (see above). The regression coefficient for a given time period, once back-transformed, estimates the constant percent change for the specified time period

(Nur et al. 1999b). Our objective was 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 will occur. We therefore chose the last 5-6 years for this exercise. Population trends in the period before 2006 are less relevant for this exercise because Burrowing Owl abundance and Burrowing Owl predation on Ashy Storm-Petrels were much lower in the first half of the 2000's (2001-2006) than in the most recent 5-6 years. To obtain a more robust estimate of the recent time period we used two possible time periods 2007-2011 (last 5 yrs of mist net data, a 4 yr-interval) and 2006-2011 (last 6 yrs, a 5 yr-interval). We then took the geometric mean of the two estimates; Percent change over time is multiplicative and therefore the geometric mean, not the arithmetic mean is the appropriate mean to use (Nur et al. 1999b). The geometric mean was used to model the current period.

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 2011, 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 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 Owl 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, i.e., the one that optimized AIC, and use these results for inclusion in the 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. (1999) 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 is described in this report. We then incorporated changes in adult survival associated with presumed changes in Burrowing Owl abundance on the Farallon Islands. These changes in Burrowing Owl abundance in turn reflect the likely consequences of proposed mouse eradication. The second step was to model the population dynamics of Ashy Storm-Petrels, given the presumed, statistically estimated, changes in survival.

The changes in adult survival were directly estimated from the statistical analysis of the 12-year dataset (capture histories from 2000 to 2011) 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 a population dynamic model that accounted for recently observed population trends; the postulated post-eradication parameter values reflect 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. (1999) 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 a population that exhibited the same population trajectory as has recently been observed (a decline of approximately 3% per year, see “Results”).
- ii) **Survival of juveniles and subadults.** We followed Nur et al. (1999), 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. (1999) 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. (1999) and use this value.
- v) **Probability of Breeding for the First Time.** No field data are available to estimate this parameter for this species (Ainley 1995). Here we followed Nur et

al. (1999) who relied on a field study of the closely related Leach's Storm-Petrel (*O. leucorhoa*). Nur et al. (1999) assumed that, for the Farallon Ashy Storm-Petrel population, 10% of four-year olds, 50% of five-year olds, 90% of six-year olds, and 100% of seven-year olds were capable of breeding. 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 (Warzybok et al. 2009), but which then return to their natal colonies when they reach maturity (Nur & Sydeman 1999). Nur et al. (1999) 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. 1999). 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

Sydeman, et al. (1998b), reviewed and updated by Nur et al. (1999a), estimated a breeding population of 2,660 on SEFI in 1992. Nur et al. (1999a) assumed 53.5% of the population were breeders, and therefore they estimated a total population size of 4,972 birds. For current population size for the purposes of the modeling, we relied on the mist-net based population index, as described above. Using data from the last 3 years (2009-2011), the number of captures (after controlling for mist netting site, mist netting effort, and date) was 75% to 171% greater in 2009-2011 than in 1992, depending on year. The geometric mean of the three annual index values corresponds to a 128.2% increase over the 1992 value. Hence, we estimate a breeding population of 6070 individuals for the most recent 3-year period ($= 2,660 \times 2.282$). In other words, we assumed the proportion of breeders to non-breeders in the mist netting sample did not differ among years. Given 6,070 breeding individuals and 53.5% of the total population consisting of breeders (Nur et al. 1999a), this implies an estimated total population of 11,346 birds for the period 2009-2011. The population model used a starting total population size in “Year 0” of 11,346 individuals, equivalent to a breeding population of 6,070 birds.

Population model matrix: population size and calibration

Population projections were carried out using the initial population size (see above) and an age-based Leslie matrix assuming a pre-breeding census (Caswell 2000). The elements of the Leslie matrix were constant over time. Reproductive success was based on recent (10-year) observations in the field (see above). Survival of adults was calibrated to yield a lambda value that matched the “recent observed” value (see above). Note that adjustment of adult survival also resulted in proportional adjustment

of survival rates of first-year and sub-adults (i.e., individuals in their second and third year of life). As noted, fourth-year individuals were presumed to display adult survival values.

Population model matrix: modeling impacts of Burrowing Owl predation

The result of the calibration process was that the population dynamic model reproduced recent behavior of the population, the most recent 5 to 6 years. These are conditions under which Burrowing Owl abundance has been relatively high. Thus, we used the “recent population dynamic model” to represent the baseline condition scenario: that is, the expected population trend in the near future if there was no change in abundance of Burrowing Owl on the island. The “recent” model is one in which we assume that current conditions continue into the future, specifically, 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 (see above).

We analyzed the most recent 3 years of data 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 3 most recent years. The mean maximum number of Burrowing Owls observed per month over the 8-month observation period, September to April (see above) was 6.29. The 71.5% reduction scenario involves reducing Burrowing Owl abundance by an amount equivalent to the mean observed per month over just the most recent year, from September 2011 to April 2012. 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 mean maximum number of Burrowing Owls observed per month.

We suspect that migrating Burrowing Owls may still errantly 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 time when no readily 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 are present in low numbers during those months. Furthermore, 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, as per our statistical estimate. For the purposes of modeling we assumed that second-year birds were absent from the island, but that third-year birds were present, mostly as pre-breeders. 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 (and therefore not subject to Burrowing Owl predation). Our mist-net data for storm petrels contains very few birds banded as chicks, and so are of known 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 scenarios of reduction in Burrowing Owl abundance: a) No owl reduction, b) 50% owl reduction and c) 71.5% owl reduction. 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), house mouse populations are at very high levels (September is the second-highest month for house mouse abundance). 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 few Ashy Storm-Petrels are still breeding in those months (Ainley et al. 1990).

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 pattern suggests that when mice are available, Ashy Storm-Petrels are not the primary prey for Burrowing Owls.

Annual Variation in Population Size and Predation

Variation in Index of ASSP Population Size

The Ashy Storm-Petrel population index displayed marked year-to-year variation from 2001 to 2011, and much less variation from 1992 to 2001 (Figure 3). The estimated annual rate of decline for the period 2007-2011 was 5.46%, i.e., $\Lambda = 0.9454$; the estimated decline for 2006-2011 was 0.78% per year, i.e., $\Lambda = 0.9922$. The geometric mean of the two rates is 3.15% decline. We therefore used a Λ of 0.9685 to model recent population trends. The estimated decline of 3.15% per year was not much different from the 2.78% per year decline estimated by Sydeman et al. (1998a) for the earlier time period, 1972 to 1992. Ainley and Hyrenbach (2010) estimated a substantial decline over the period 1985 to 2006 for the Central California population, based on at sea surveys. Analyzing the population index for SEFI 1992 to 2001, the estimated decline was 4.99% per year (Figure 3). From 2001 to 2007, the population increased by 22.48% per year; it declined by 5.46 % per year from 2007 to 2011.

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 4). 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 (Figure 4). Note that the the four highest years of abundance have been the four most recent years (2009-2012).

Burrowing Owl Predation on Ashy Storm-Petrels

The results of the analysis show that Burrowing Owl predation on Ashy Storm-Petrels has increased over time (Figure 5). 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 Ashy Storm-Petrel Survival Probability

The analysis of Ashy Storm-Petrel survival was restricted to 2000-2011 to match the period of time for which the Burrowing Owl abundance index was available. We also considered survival values for the 1990's to be less relevant than those since 2000, for the purposes of modeling future population responses.

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 factors affecting survival: Sept-April index

of Burrowing Owl abundance and location of mist-netting site (LHH vs. CS). The optimal model also included two factors affecting recapture probability: site and winter SOI. The coefficients and other statistics for the optimal model are depicted in Table 2.

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 2). Therefore a reduction in the Burrowing Owl index by 50% is expected to increase logit survival by 0.356. A reduction in the Burrowing Owl index by 71.5% is expected to increase logit survival by 0.509. The change in adult survival associated with the three scenarios was calculated and is presented in Table 3. 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”) is associated with an absolute increase in survival of 0.7% to 1.1%, depending on the baseline value of survival. Thus, 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), is expected to increase adult storm-petrel survival by 0.033 or a relative 3.73% for adults; a 71.5% reduction in Burrowing Owl abundance (equal to reduction in the index of 4.5 owls) is expected to increase adult storm-petrel survival by 0.044 or a relative 5.0% for adults (Table 3).

The expected relative change in Petrel mortality as result of owl reduction (Table 3) is clear:

- A 50% reduction in Burrowing Owl abundance is expected to result in a 27% decrease in overall Ashy Storm-Petrel mortality, from all causes.
- A 71.5% decrease in Burrowing Owl abundance is expected to produce a 37% decrease in Ashy Storm-Petrel mortality, from all causes.

Population Dynamic Model

We developed a population dynamic model for Ashy Storm-Petrels that produced a population that declines at 3.15% per year, corresponding to the most recent 5 – 6 years. The demographic parameter values are listed and annotated in Table 4. Adult survival value of 88% is consistent with an observed population decline of 3.15%, given

the other parameter values including an estimate of reproductive success from the most recent 10 years.

We then modified survival of all individuals beyond second-year individuals (see Methods) under the two “Burrowing Owl reduction scenarios.” The new adult survival values are depicted in Table 3. The new lambda values under the two Burrowing Owl reduction scenarios are also depicted in Table 3. Changes in ASSP population size for the three scenarios over a twenty year time period are displayed in Figure 6.

The most important results to emerge from this analysis are:

- 1) With no mouse removal and no resulting reduction in Burrowing Owl abundance (i.e., assuming recent conditions continue into the future) the ASSP population is expected to decrease by 27.4% over a 10 year period. This is equivalent to a loss in the breeding population of 1,663 individuals compared to current levels (4,407 vs 6,070).
- 2) A 50% reduction in Burrowing Owl abundance can be expected to change an ASSP population that declines by 27.4% into one that is approximately stable; the estimated ASSP population trend under the 50% owl reduction scenario is an increase of about 0.1% per year. After 10 years, the difference in the ASSP breeding population between 0% and 50% reduction of Burrowing Owl abundance is 1,706 individuals. The ASSP population is projected to have increased by 0.7% after 10 years (6,113 vs 6,070).
- 3) With a 71.5% reduction in the index for Burrowing Owl abundance, an increasing ASSP population is expected, increasing at a rate of 1.1% per year. After 10 years, the difference in the ASSP breeding population between 0% and 71.5% reduction of Burrowing Owl abundance is 2378 individuals. The ASSP population is projected to increase by 11.8% after 10 years (6,785 vs 6,070).

Discussion

Our statistical analysis demonstrates that observed changes 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 changes 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 will likely turn an Ashy Storm-Petrel population declining at 27.4% into a stable one. A reduction of recent Burrowing Owl abundance by substantially over 50% will allow Ashy Storm-Petrel populations on SEFI to increase. These results are quantitative evidence supporting the expected benefits to the Ashy Storm-Petrel population from the proposed house mouse eradication on the Farallones, which is 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 for Burrowing Owl. Burrowing owls prefer mice as prey, and prey on storm-petrels when mice are not available. Both the monthly and annual data demonstrate that more Burrowing Owl 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 abundance index), is expected to increase storm-petrel survival by approximately 1%; a 50% reduction in owl abundance is expected to increase survival by more than 3%, which is equivalent to reducing annual mortality by 27%. 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. 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 convincing 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 potential changes in Burrowing Owl abundance.

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. 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.

Our population dynamic model produced a population that declined at a rate corresponding to the recent 5-6 year period. Preliminary examinations of 2012 mist-data suggest this decline has continued (PRBO unpublished). However, it is clear from our population index values that though the population declined from 1992 to 2001, there was a large increase in storm-petrel mistnet captures between 2001 and 2007, when the index increased by 3 times. The nature of this increase is unclear, but corresponded with large population increases in other seabird species which demonstrated strong population growth during consistent productive ocean conditions in the early 2000's (Warzybok and Bradley 2010). The important point is that the population trend from 2007 to 2011 is significantly different from the trend observed 2001 to 2007 ($t = -2.77$, $df = 8$, $P = 0.024$, change-point analysis of 2001 to 2011 comparing trend to 2007 with trend since 2007). The reversal of this rapid growth starting in 2007, resulting in decline, is associated with observations of high Burrowing Owl abundance and high predation on storm-petrels in the most recent years, suggesting further evidence of the impacts of increased Burrowing Owl abundance and predation on storm-petrels.

It is rare in ecological studies to have direct evidence of variation in predation rates that is 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 causal, quantitative relationship between owl abundance and Ashy Storm-Petrel survival rates elucidated here is strong. The longer current levels of owl predation continue, the less likely this population is to recover. 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 ASSP, a very large number of Western Gulls would need to be removed from the island. Since the South Farallones host the world's largest Western Gull breeding population, numbering in the tens of thousands, and because Western gulls are a resident, native breeding species, there are no plans,

intentions nor mandate for the USFWS to attempt to manage the population of Western Gulls on the Farallones. Reducing gull predation would also 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 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 response by the 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. 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 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 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.

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). One justification is that the Southern Oscillation Index did not demonstrate a significant effect on adult survival. Secondly, 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 David and Lucile Packard Foundation. This is PRBO contribution # 1880.

References

- 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., and R.J. Boekelheide, editors. 1990. *Seabirds of the Farallon Islands: Ecology, Dynamics, and Structure of an Upwelling-System Community*. Stanford University Press.
- 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., Podolsky, R., Deforest, L., Spencer, G., and Nur, N. 2001 The status and population trends of the Newell's shearwater on Kauai: insights from modeling. *Studies of Avian Biology* 22: 108-123.
- 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.
- Angel, A., R. Wanless, and J. Cooper. 2009. Review of impacts of the introduced house mouse on islands in the Southern Ocean: are mice equivalent to rats? *Biological Invasions* 11:1743-1754.
- Bradley, R.W., and P. Warzybok. 2003. Longevity record for Ashy Storm-Petrel. *North American Bird Bander*. 28:3.
- Bradley, R., P. Warzybok, D. Lee, and J. Jahncke. 2011. Assessing Population Trends of the Ashy Storm-Petrel on Southeast Farallon Island, California. Unpublished report to the US Fish and Wildlife Service. PRBO Conservation Science, Petaluma, California. PRBO Contribution Number 1780.
- Bronson, F.H. 1979. The reproductive ecology of the house mouse. *Q Rev Biol.* 54:265-99.
- Brooke, M.D.L, and Hilton, G.M. 2002 Prioritizing the world's islands for vertebrate eradication programs. *Aliens* 16, 12–13.
- Cameron, A.C., and Trivedi, P.K., 1998. *Regression Analysis of Count Data*. Cambridge University Press, Cambridge, 432pp.

Carter, H.R., W.R. McIver, and G.J. McChesney. 2008. Ashy Storm-Petrel (*Oceanodroma homochroa*) in Shuford, W. D., and T. Gardali, editors. 2008. *California Bird Species of Special Concern: A ranked assessment of species, subspecies, and distinct populations of birds of immediate conservation concern in California*. Studies of Western Birds 1. Western Field Ornithologists, Camarillo, California, and California Department of Fish and Game, Sacramento.

Caswell, H. 2001. *Matrix population models*. Second edition. Sinauer Associates, Sunderland.

Cooch, E., R. Pradel, and N. Nur. 1996. *A Practical Guide to Capture/Recapture Analysis using SURGE*. 125 pages. Centre d'Ecologie Fonctionnelle et Evolutive - CNRS, Montpellier, France.

DeSante, D. and D. Ainley. 1980. The Avifauna of the South Farallon Islands, California. Studies in Avian Biology No. 4, Cooper Ornithological Society, Lawrence, KS.

Girman, D., W. J. Sydeman, and T. B. Smith. 1999. Population Genetic Structure of Ashy Storm-Petrels. Chapter 2 in Nur, N., Sydeman, W.J., Girman, D., Smith, T.B., and Gilmer, D. 1999a. *Population status, prospects, and risks faced by two seabirds of the California Current: the Ashy Storm-petrel, Oceanodroma homochroa, and Xantus' Murrelet Synthliboramphus hypoleucus*. Report to U.S. Geological Survey, Biological Resources Division.

Gervais, J.A. D.K. Rosenberg, and L.A. Comrack. 2008. Burrowing Owl (*Athene cunicularia*). In: Shuford, W.D. and Gardali T., editors: *California Bird Species of Special Concern: A ranked assessment of species, subspecies, and distinct populations of birds of immediate conservation concern in California*. Studies of Western Birds 1. Western Field Ornithologists, Camarillo, California, and California Department of Fish and Game, Sacramento.

Hilbe, J., 2007. *Negative Binomial Regression*. Cambridge University Press, Cambridge, UK.

Howald, G., Donlan C. J., Galvan, J. P., Russell, J. C., Parkes, J., Samaniego, A., Wang, Y., Veitch, D., Genovesi, P., Pascal, M., Saunders, A. and Tershy, B. 2007. Invasive Rodent Eradication on Islands. *Conservation Biology* 21: 1258–1268.

Huntington, C. E., R. G. Butler, and R. A. Mauck. 1996. Leach's storm-petrel (*Oceanodroma leucorhoa*). In *The Birds of North America, No. 233* (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences, Philadelphia, PA and The American Ornithologists Union, Washington, D.C.

Irwin, J. 2006. The impact of house mice on ashby-storm petrels on Southeast Farallon Island, Unpublished report to U.S. Fish and Wildlife Service. Farallon National Wildlife Refuge, Fremont, CA.

Krajick R. 2005 Winning the war against island invaders. *Science* 310, 1410–1413.

Laake, J., E. Rakimberdiev, B. Collier, J. Rotella and A. Paul. 2012. RMark: R Code for MARK Analysis. R package version 2.1.0. <http://CRAN.R-project.org/package=RMark>

Lee, D. E., N. Nur, and W. J. Sydeman. 2007. Climate and demography of the planktivorous Cassin's auklet *Ptychoramphus aleuticus* off northern California: implications for population change. *Journal of Animal Ecology* 76:337-347.

Mills, K. 2006. Owl diet on Southeast Farallon Island, 1996-2004. Unpublished PRBO report to USFWS.

Mulder, C.P.H., W. B. Anderson, D. R. Towns and P. J. Bellingham(Eds). 2011. Seabird Islands: Ecology, Invasion, and Restoration. Oxford University Press, Oxford . 512 pp.,

Nur, N. and G. R. Geupel. 1993. Evaluation of mistnetting, nest-searching and other methods for monitoring demographic processes in landbird populations. pp. 237-244 in *Status and Management of Neotropical Migrant Birds* (ed. by D. Finch and P. Stangel). USDA Forest Service Gen. Techn. Rep. RM-229. USDA, Fort Collins, CO.

Nur, N. and W.J. Sydeman. 1999. Demographic processes and population dynamic models of seabirds: Implications for conservation and restoration. *Current Ornithology* 15:149-188.

Nur, N., W. J. Sydeman, D. Girman, T. B. Smith, T.B., and D. Gilmer. 1999a. Population status, prospects, and risks faced by two seabirds of the California Current: the Ashy Storm-petrel, *Oceanodroma homochroa*, and Xantus' Murrelet *Synthliboramphus hypoleucus*. Report to U.S. Geological Survey, Biological Resources Division.

Nur, N. S.L. Jones, and G.R. Guepel,. 1999b. Statistical Guide to Data Analysis of Avian Monitoring Programs. Biological Technical Publication, US Fish and Wildlife Service, BTP-R6001-1999.

Nur, N., D.E. Lee, R.W. Bradley, P.M. Warzybok, and J. Jahncke. 2011. Population Viability Analysis of Cassin's Auklets on the Farallon Islands in relation to environmental variability and management actions. Unpublished report to the National Fish and Wildlife Foundation and the US Fish and Wildlife Service. PRBO Conservation Science, Petaluma, California. PRBO Contribution Number 1793.

Nur, N., R.W. Bradley, D.E. Lee, P.M. Warzybok, and J. Jahncke. 2012. Population Viability Analysis of Western Gulls on the Farallon Islands in Relation to Potential

Mortality Due to Proposed House Mouse Eradication. Unpublished report to the US Fish and Wildlife Service. PRBO Conservation Science, Petaluma, California. PRBO Contribution Number 1868.

Richardson, T., P. Pyle, R. Burnett, and P. Capitolo. 2003. The occurrence and seasonal distribution of migratory birds on Southeast Farallon Island, 1968-1999. *Western Birds* 34:58-96

Schoener, T.W., Spiller, D.A., 1996. Devastation of prey diversity by experimentally introduced predators in the field. *Nature* 381, 691–694.

Spear, L. B., and D.G. Ainley. 2007. Storm-petrels of the eastern Pacific Ocean: Species assembly and diversity along marine habitat gradients. *Ornithol. Monogr.* 62.

Sydeman, W.J., N. Nur, E.B. McLaren, and G.J. McChesney. 1998a. Status and trends of the Ashy Storm-petrel on Southeast Farallon Island, California, based upon capture-recapture analyses. *The Condor*, 100: 438-447.

Sydeman, W.J., Nur, N., and Martin, P. 1998b. Population viability analyses for endemic seabirds of the California marine ecosystem: the ashy storm-petrel (*Oceanodroma homochroa*) and Xantus' murrelet (*Synthliborhamphus hypoleucus*). PRBO Report to U.S. Biological Resources Division, Species at Risk Program.

Wanless, R., A. Angel, R. Cuthbert, G. Hilton, and P. Ryan. 2007. Can predation by invasive mice drive seabird extinctions? *Biology Letters* 3:241-244.

Wanless, R. M., Ratcliffe, N., Angel, A., Bowie, B. C., Cita, K., Hilton, G. M., Kritzing, P., Ryan, P. G., Slabber, M. (2012), Predation of Atlantic Petrel chicks by house mice on Gough Island. *Animal Conservation*.

Warzybok, P., R. Bradley, and S.N.G. Howell. 2009. First North American record of Tristram's Storm-Petrel (*Oceanodroma tristrami*). *North American Birds* 62(4):2-4.

Warzybok, P.M. and R.W. Bradley. 2010. Population Size and Reproductive Performance of Seabirds on Southeast Farallon Island, 2010. Unpublished report to the US Fish and Wildlife Service. PRBO Conservation Science, Petaluma, California. PRBO Contribution Number 1768.

Weimerskirch, H. 2002. Seabird demography and its relationship with the marine environment pp. 115-136 in *Biology of Marine Birds*, (E. A. Schreiber and J. Burger, Eds.). CRC Press, Boca Raton.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. *Bioscience* 48: 607–615.

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_{adj} .

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. 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 CI	Upper 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: $\text{LRS} = 6.743$, $\text{df} = 1$, $P = 0.009$.

Table 3. 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 2000-2011.

Change in Burrowing Owl Index	Adult Survival	Change in Survival	Percent Change in Mortality	Lambda	Change in Lambda	Population Growth Rate	Description
0	0.8800	0	0	0.9685	0	3.15% decline	Recent trend, no change in Burrowing Owl
Decrease by 3.145	0.9128	0.0328	27%	1.0007	0.0322	0.07% increase	Recent trend; decrease by 50% of recent mean
Decrease by 4.5	0.9242	0.0442	37%	1.0112	0.0427	1.12% increase	Recent trend; decrease by 72% of recent mean

Table 4. Ashy Storm-Petrel Demographic Parameter Values Used to Model Current Conditions: No Burrowing Owl Reduction

Age	Proportional Survival to Mature Adult ¹	Survival ²	Breeding Probability ³	Breeding Success ⁴
1	0.72	0.6336	0	0
2	0.86	0.7568	0	0
3	0.98	0.8624	0	0
4	1	0.88	0.092	0.588
5	1	0.88	0.46	0.588
6	1	0.88	0.828	0.588
7	1	0.88	0.92	0.588
8	1	0.88	0.92	0.588
9	1	0.88	0.92	0.588
10	1	0.88	0.92	0.588
11	1	0.88	0.92	0.588
12	1	0.88	0.92	0.588
14	1	0.88	0.92	0.588
14	1	0.88	0.92	0.588
15	1	0.88	0.92	0.588
16+	1	0.863	0.92	0.588

¹ - From Nur et al. 1999a

² - Adult survival calibrated to produce population $\lambda = 0.9645$

³ - Product of mature adult breeding probability and probability of breeding for the first time

⁴ - Mean value, SEFI, 2002-2011

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

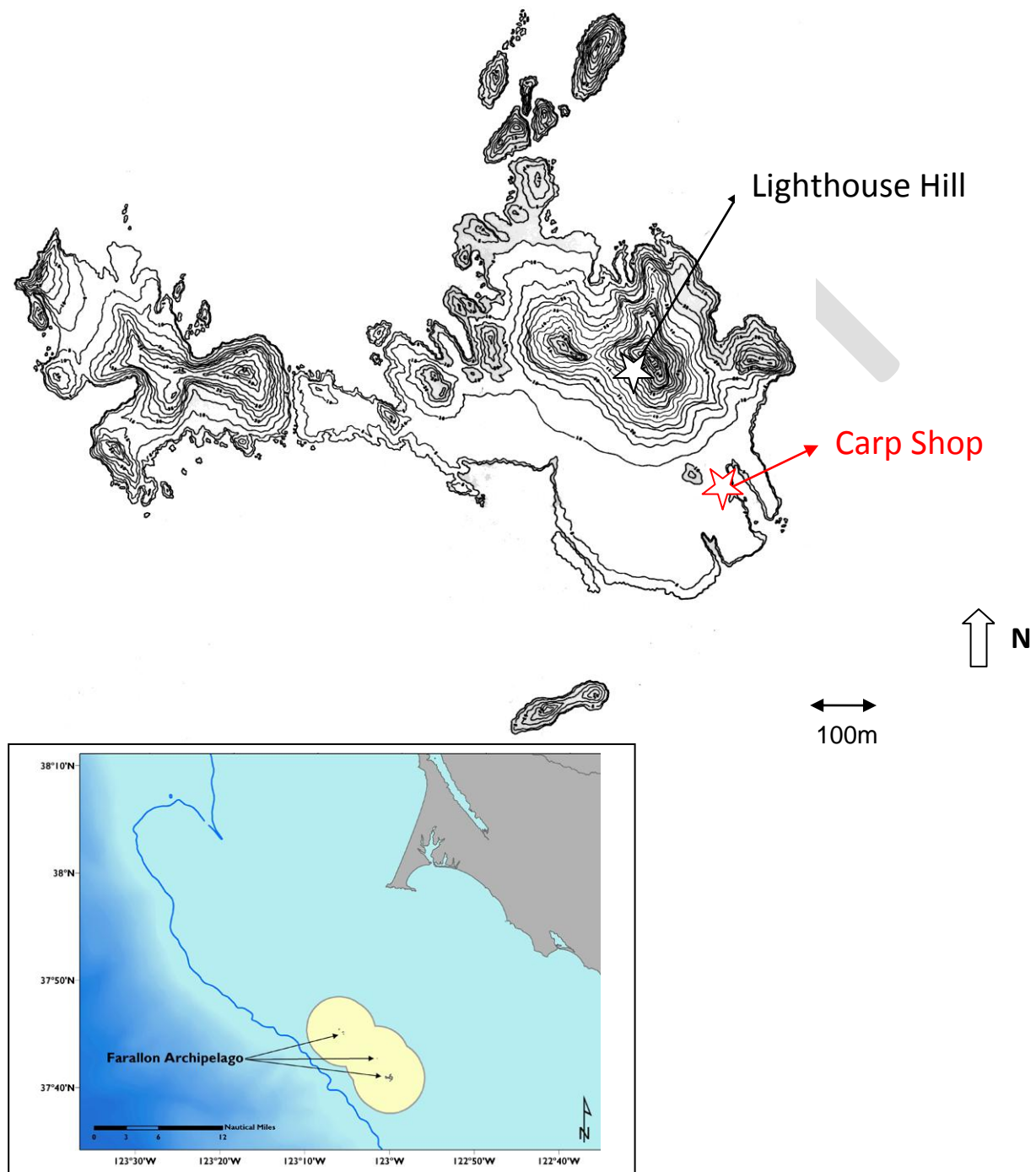


Figure 2. Seasonal Cycle of House Mouse Abundance (2001-2004, 2011-2012), Ashy Storm-Petrel predation by Burrowing Owl (2008-2012), and Burrowing Owl abundance (2008-2012) at Southeast Farallon Island. Monthly values with standard deviation are shown.

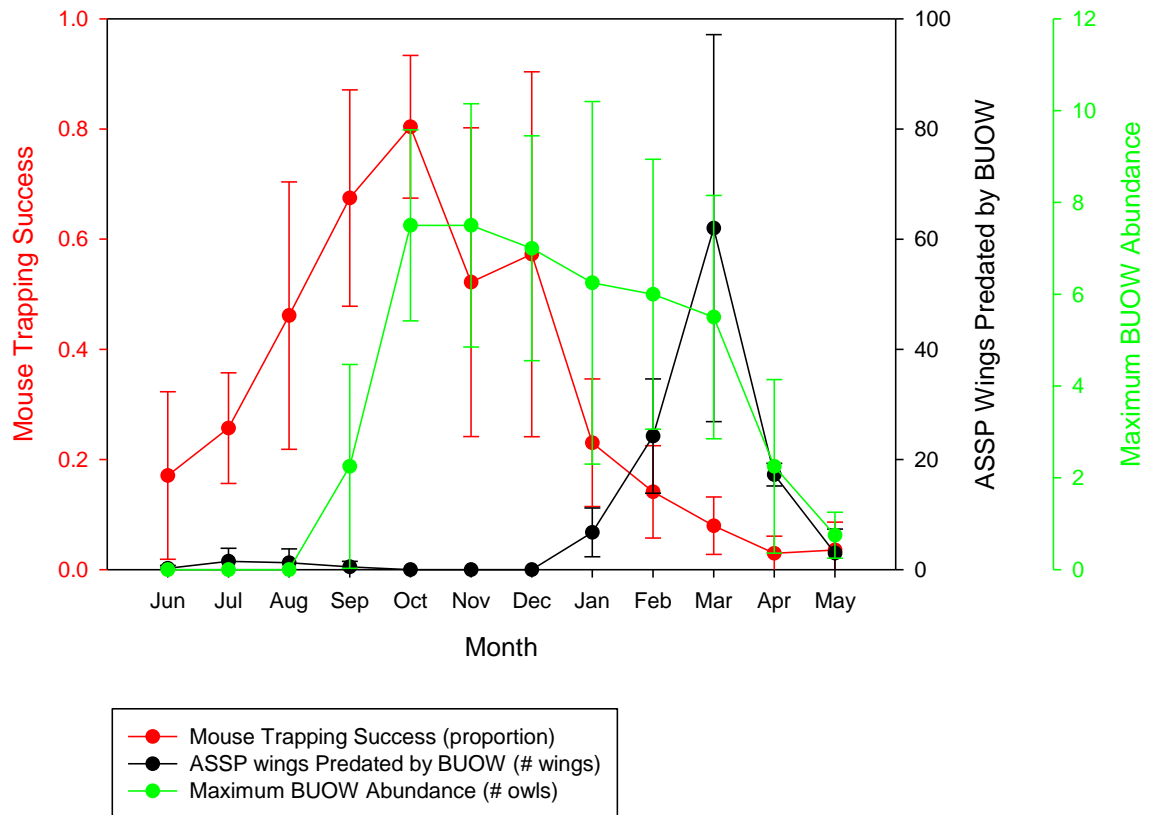


Figure 3. Population Index from Mist-netting Analyses for Ashy Storm-Petrels, 1992 to 2011 from Southeast Farallon Island. The index is set at 1.0 for 1992 (see Methods). Index values are presumed directly proportional to abundance of Ashy Storm-Petrels.

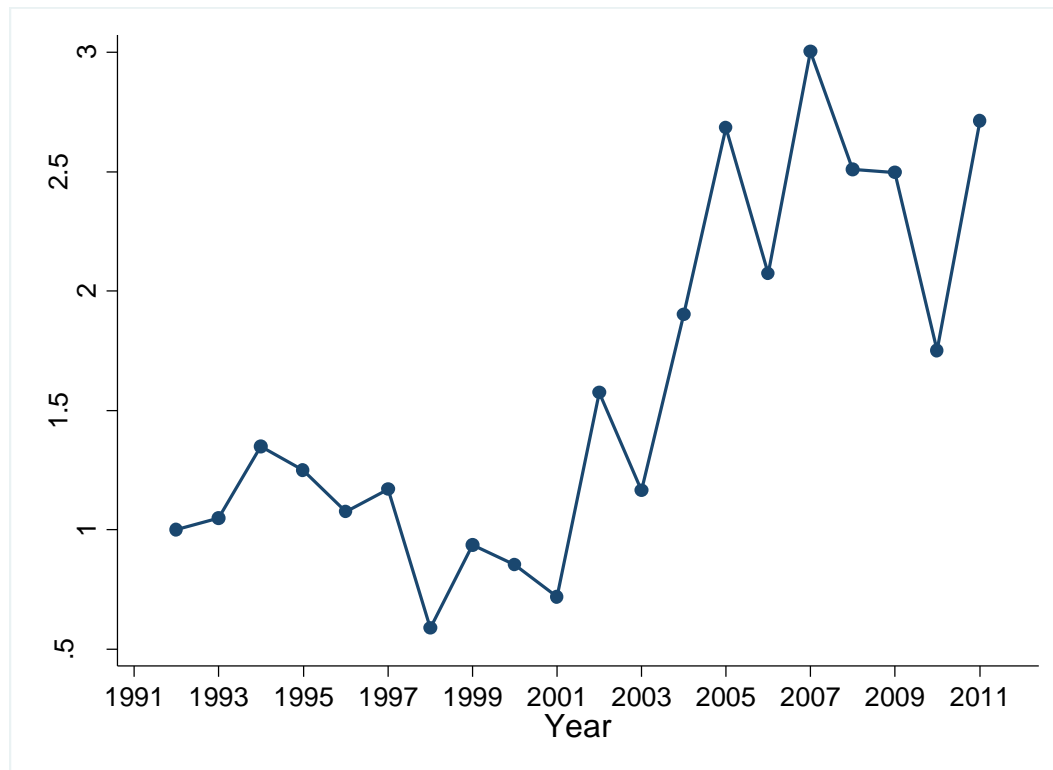


Figure 4. Variation in the annual Burrowing Owl abundance index (mean Sept-April abundance) for 2001 to 2012 on Southeast Farallon Island. The curve of best fit, as determined by AIC, is shown: a quadratic, accelerating trend.

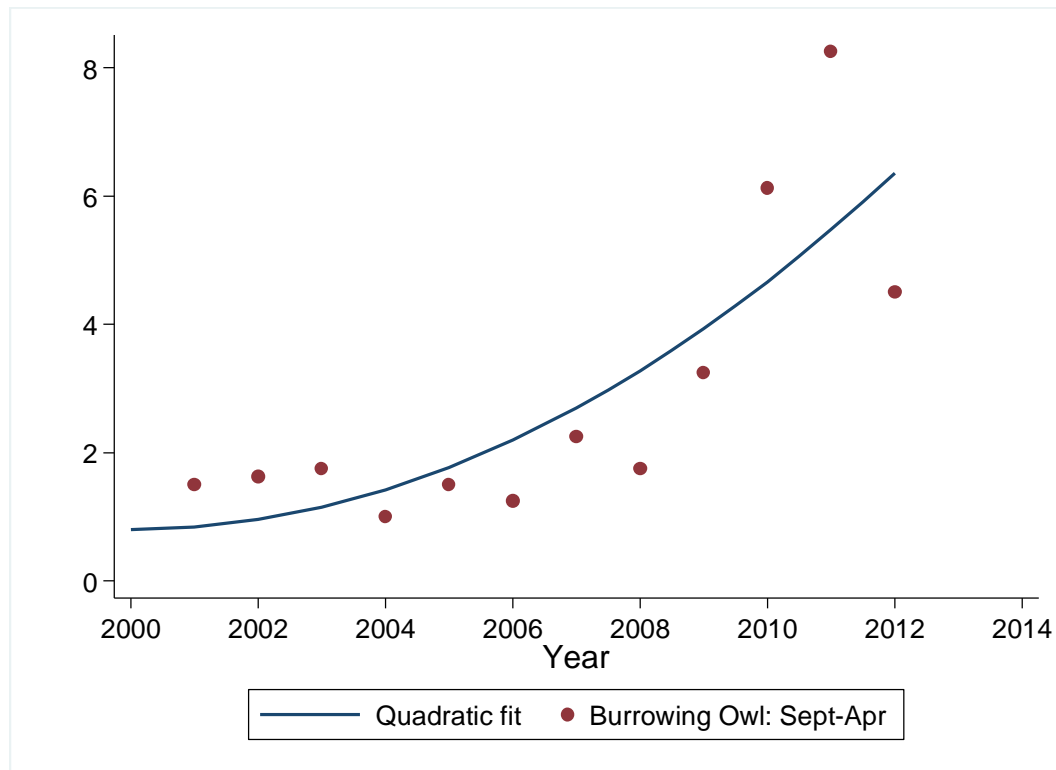


Figure 5. Ashy Storm-Petrel Burrowing Owl Predation Index from 2003 to 2011 on Southeast Farallon Island. The curve of best fit, as determined by AIC, is shown: a quadratic, accelerating trend.

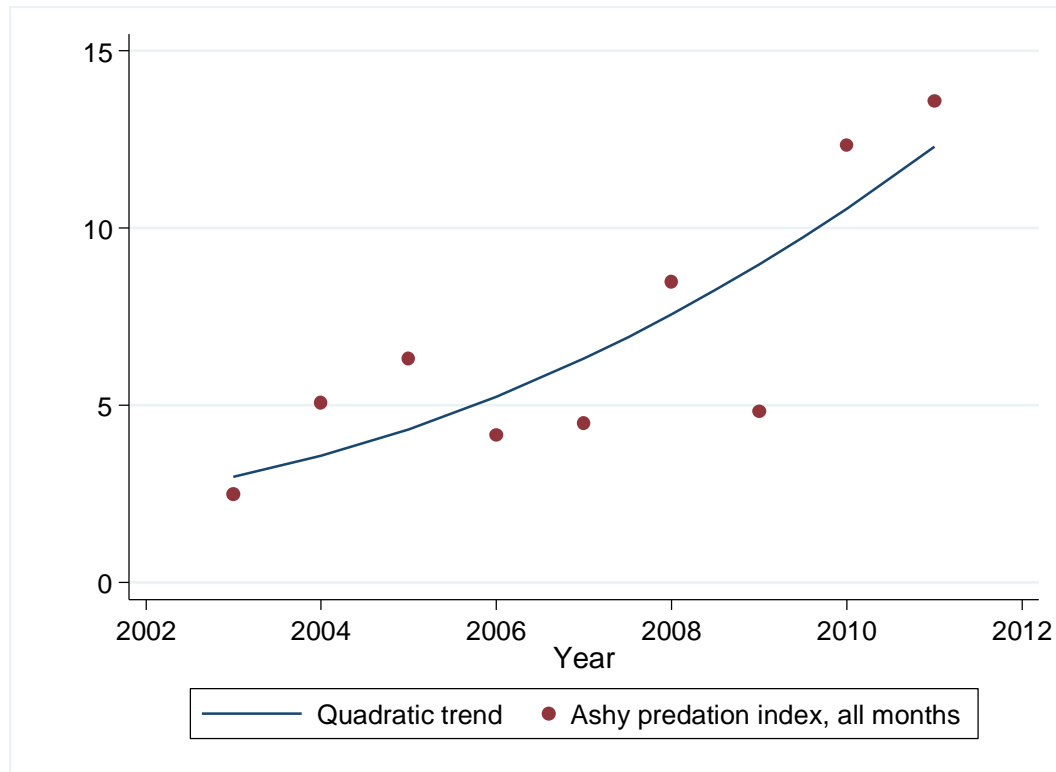


Figure 6. Farallon Ashy Storm-Petrel Population projections under the three scenarios of reduction in Burrowing Owl Abundance: 0% reduction, 50% reduction, and 71.5% reduction. Depicted are estimated breeding population sizes for a 20-year period. Year 0 corresponds to most recent conditions and is the year that Burrowing Owl reduction occurs. Starting population size is 6,070 in Year 0 (see text).

