

Articles

Response of Native Species 10 Years After Rat Eradication on Anacapa Island, California

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Abstract

Measuring the response of native species to conservation actions is necessary to inform continued improvement of conservation practices. This is particularly true for eradications of invasive vertebrates from islands where up-front costs are high, actions may be controversial, and there is potential for negative impacts to native (“nontarget”) species. We summarize available data on the response of native species on Anacapa Island, California, 10 y after the eradication of invasive black rats *Rattus rattus*. Native marine taxa hypothesized to respond positively to rat eradication increased in abundance (Scripps’s murrelet *Synthliboramphus scrippsi*; International Union for Conservation of Nature Vulnerable, and intertidal invertebrates). Two seabird species likely extirpated by rats—ashy storm-petrel *Oceanodroma homochroa* (International Union for Conservation of Nature Endangered) and Cassin’s auklet *Ptychoramphus aleuticus*—are now confirmed to breed on the island. Long-term negative effects from nontarget impacts are limited. Rufous-crowned sparrows *Aimophila ruficeps obscura* are still present, although likely in lower abundance. The endemic Anacapa deer mouse *Peromyscus maniculatus anacapae* population increased with no loss in heterozygosity, but with reduced genetic differentiation on East Anacapa and the loss of some alleles across the islets. Intertidal invertebrate cover increased while algal cover decreased. These findings clarify the pervasive effects of invasive rats on a wide variety of taxa, the short- and long-term impacts of eradication, and the ability of some island fauna to passively recover following a carefully planned rat-eradication project.

Keywords: Anacapa deer mouse; ashy storm-petrel; introduced predator eradication; long-term monitoring; post-eradication recovery; *Rattus rattus*; Scripps’s murrelet

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Introduction

The world may be in the midst of an extinction crisis that has negative economic, ethical, and aesthetic effects and is permanent over time scales relevant to humans (Pimm et al. 2006; Wake and Vredenburg 2008). For well-studied taxa, current extinction rates are two to three orders of magnitude greater than background rates and above rates at which new species evolve (Dirzo and Raven 2003). Sixty-one percent of extinct species (International Union for Conservation of Nature Extinct) were confined to islands, where the extinction was caused, at least in part, by invasive species (IUCN 2015; Tershy et al. 2015).

Efforts to prevent extinctions by eradicating invasive species from islands are increasingly common and complex, with approximately 12 island eradications/y over the past decade, some on larger, more biologically diverse islands (Keitt et al. 2011). Although the benefits of invasive species eradication are well-documented (Bellingham et al. 2010; Veitch et al. 2011), the long-term effects of these efforts are rarely evaluated (Sutherland et al. 2004; Ferraro and Pattanayak 2006). Failure to evaluate the outcomes of conservation actions limits the potential for data-driven, iterative improvements in conservation. Furthermore, without data on outcomes, conservation funders and practitioners are unable to prioritize islands where eradication or other actions will have the greatest benefits for biodiversity.

Introduced rats *Rattus* spp. are the most widespread invasive vertebrate on islands where they have direct and indirect effects on native fauna (Shiels et al. 2014). For birds, direct effects of rats include predation of eggs, chicks, and adults (Atkinson 1985; Jones et al. 2006), with effects ranging from reduced recruitment to total extinction (Townsend et al. 2006). Black rats *Rattus rattus* have greater impacts on seabirds than do other *Rattus* species, with particularly severe effects on burrow-nesting seabirds such as storm-petrels (Hydrobatidae; Townsend et al. 2006; Jones et al. 2008). In addition to predation on birds, black rats impact native rodents (Harris and Macdonald 2007) through predation and competition for food (Ozer et al. 2011). Rats are also known to directly affect reptiles and amphibians by preying on eggs and juveniles (Townsend et al. 2006; Townsend 2009; Traveset et al. 2009). Rats either have direct effects on intertidal invertebrate communities via predation (Erickson and Halvorson 1990; Smith et al. 2006) or indirect effects via direct predation on birds that forage in the intertidal (Kurle et al. 2008).

Invasive rats are the most frequent target of eradication efforts on islands, with >650 populations successfully removed from islands globally (Keitt et al. 2011; DIISE 2015; Russell and Holmes 2015). Black rats were eradicated from Anacapa Island, Channel Islands National Park, California in November 2002 with the goal to

improve seabird nesting habitat and aid in the recovery of Scripps's murrelet (*Synthliboramphus scrippsi*, formerly Xantus's murrelet (Birt et al. 2012; Chesser et al. 2012)) and ash storm-petrel (*Oceanodroma homochroa*) (NPS 2000). Howald et al. (2009) reported on the short-term (0–5 y post-eradication) effects including negative impacts on native vertebrates. The authors hypothesized that these negative impacts were ephemeral, and positive benefits of the eradication would increase over the longer term.

Here we report on the long-term (10 y post-eradication) effects of rat removal. Although no formal long-term monitoring plan existed for the effects of the rat eradication, we compiled available data from a variety of studies on native species identified as likely to benefit from rat eradication and on species identified as vulnerable to negative nontarget impacts of the rodenticide used to eradicate rats (Table 1; Howald et al. 2009). In addition, we compiled available data from control islands. We expected that native species subject to direct rat predation (seabirds, landbirds, lizards, native mammals, intertidal invertebrates) would increase in abundance. We expected indirect effects on primary producers for which data were available (intertidal algae).

Study Site

Anacapa Island is in the California coastal sage and chaparral ecoregion within the Mediterranean forests, woodlands, and scrub biome (Olson et al. 2001). It is part of the Channel Islands National Park and consists of three largely cliff-surrounded islets: East (66 ha), Middle (80 ha), and West (160 ha; Figure 1). Black rats were first reported on Anacapa Island in the early 1900s (Banks 1966; Collins 1979). By 1975 all other nonnative mammals introduced to Anacapa Island (cats *Felis catus*, rabbits *Oryctolagus cuniculus*, and sheep *Ovis aries*) had been eradicated or died out (McChesney and Tershy 1998). In the late 1990s the Channel Islands National Park, the nongovernmental organization Island Conservation, and the American Trader Trustee Council (consisting of the California Department of Fish and Wildlife, U.S. Fish and Wildlife Service, and the National Oceanic and Atmospheric Administration) partnered to plan the rat eradication. Because the effort was funded by oil-spill restoration funds, there was an emphasis on threatened seabird recovery, including Scripps's murrelet (World Conservation Union RedList Vulnerable; IUCN 2015) and ash storm-petrel (World Conservation Union RedList Endangered; IUCN 2015) because of the effects the American Trader oil spill had on those two species (ATTC 2001). The rat eradication (2001–2002), summarized by Howald et al. (2009), was the first aerial application of rodenticide in North America, the first globally on an island with an endemic rodent (Howald et al. 2005), and was staged in



Table 1. Species and years of pre- and post- rat eradication monitoring data on Anacapa Island, California.

| Species | Scientific name | Pre-eradication | Post-eradication |
|------------------------------------|--|-----------------|----------------------------|
| Seabirds | | | |
| Scripps's murrelet | <i>Synthliboramphus scrippsi</i> | 2001–2002 | 2003–2010 |
| Cassin's auklet | <i>Ptychoramphus aleuticus</i> | 2001–2002 | 2003–2012 |
| Ashy storm-petrel | <i>Oceanodroma homochroa</i> | 2001–2002 | 2003–2012 |
| Reptiles and amphibians | | | |
| Southern alligator lizard | <i>Elgaria multicarinata</i> | 1993–1998, 2000 | 2003–2004, 2010–2011 |
| Channel Islands slender salamander | <i>Batrachoseps pacificus</i> | 1993–1998, 2000 | 2003–2004, 2010–2011 |
| Landbirds | | | |
| Rufous-crowned sparrow | <i>Aimophila ruficeps obscura</i> | 2002 | 2003–2005, 2007–2008, 2011 |
| Mammals | | | |
| Anacapa Island deer mouse | <i>Peromyscus maniculatus anacapae</i> | 2000–2001 | 2010–2011 |
| Intertidal community | | 1994–2002 | 2003–2010 |

two phases: East Anacapa in December 2001, and West and Middle Anacapa in November 2002. Thirty-five native vertebrate species have been reported breeding on Anacapa Island: 2 lizards, 1 amphibian, 21 land birds, 10 seabirds, and 1 mammal (NPS 2000). Of these, pre-

(prior to November 2002) and post-eradication (2003–2012) monitoring data exist for seven species as well as for the intertidal community (Table 1).

For control sites, we used two of the four other islands in the Channel Islands National Park. Santa Barbara Island

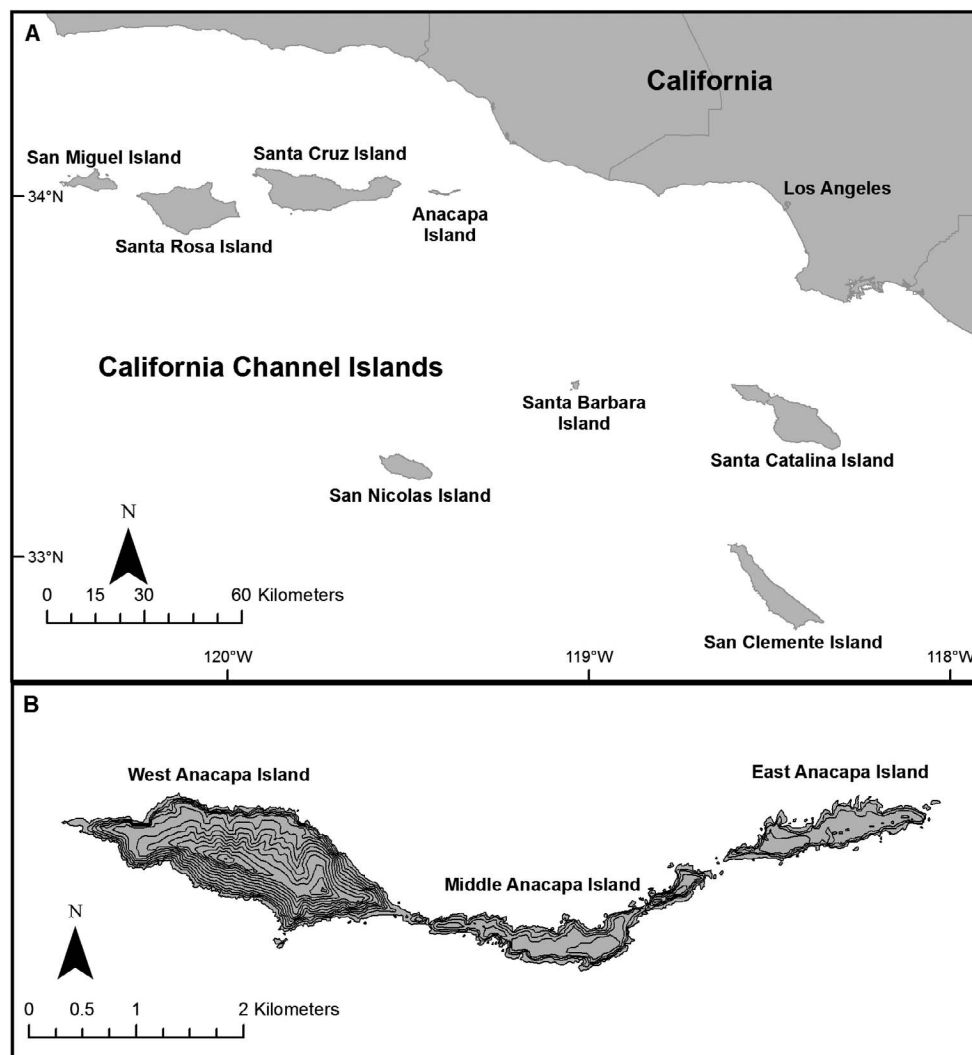


Figure 1. (A) The eight California Channel Islands, off the coast of California, USA. (B) The three Anacapa Island islets shown in detail (20-m contour lines).

(260 ha) is a suitable control island for seabird and deer mouse comparisons. Santa Barbara Island is home to breeding Scripps's murrelet, Cassin's auklet *Ptychoramphus aleuticus*, ashly storm-petrel, and deer mouse populations (Whitworth et al. 2011; Stanley 2012). Although the subspecies of deer mouse on Santa Barbara Island is different from the one on Anacapa Island, Santa Barbara Island is free of invasive mammals and, unlike the other Channel Islands, does not support any other native mammal species. In addition, monitoring data exist for the deer mouse and seabird species listed above. We used Santa Cruz Island (24,900 ha) as a control island for intertidal community comparisons. Santa Cruz Island is free of invasive mammals, and the intertidal community at the southern end of Santa Cruz Island is similar to Anacapa Island (Blanchette et al. 2009). No comparable data from control islands were available for reptiles or amphibians.

Background

Seabirds

We reviewed literature related to the post-eradication recovery of 3 of the 10 seabird species that breed on Anacapa Island: Scripps's murrelet, Cassin's auklet, and ashly storm-petrel (Table 1). Prior to rat eradication, Scripps's murrelet nests on Anacapa Island were first recorded in 1994–1996 after extensive searches of sea caves (Carter et al. 1997). At that time, they had been nearly extirpated from Anacapa Island because of rat predation (Carter et al. 1997). No active Cassin's auklet nests had been found on Anacapa Island prior to 2003, although there were signs of potential breeding (Whitworth et al. 2012; Carter and Whitworth 2013). Likewise, no ashly storm-petrel nests had ever been found on the island, but breeding was suspected based on mist-net captures (Whitworth et al. 2012; Carter and Whitworth 2013). Rat predation on alcids and storm-petrels is well-documented and occurs during every life stage (Jones et al. 2006, 2008).

Reptiles and amphibians

Anacapa Island supports Southern alligator lizard *Elgaria multicarinata*, side-blotched lizard *Uta stansburiana*, and Channel Islands slender salamander *Batrachoseps pacificus* populations (Fellers et al. 1988). Reptiles and amphibians are vulnerable to rat predation (Towns et al. 2006), and islands with rats are known to support smaller populations of lizards than islands without rats (Case and Bolger 1991). In addition, Southern alligator lizards are suspected to prey on Channel Islands slender salamanders (Hansen et al. 2005), while Channel Islands slender salamander activity at the surface is related to soil moisture from short-term rainfall condensation and fog (Schwemm 1996; Hansen et al. 2005). We used National Park Service monitoring data to assess pre- vs. post-eradication changes in alligator lizard and slender salamander population sizes. No control island data were

available for reptiles or amphibians and no data were available for the side-blotched lizard.

Landbirds

Although 21 species of landbirds breed on Anacapa Island, few monitoring data exist for any species. Pre- and post-eradication monitoring was limited to a subspecies of rufous-crowned sparrow *Aimophila ruficeps obscura* found only on Middle and West Anacapa and Santa Cruz islands (Johnson 1972). Although considered “extremely common” on Santa Cruz Island during the early 1990s, there are limited quantitative data on the abundance or distribution of rufous-crowned sparrows on Anacapa Island (Collins 2008; Howald et al. 2009). Rufous-crowned sparrows are granivorous and thus were likely to consume the grain-based rodenticide during the eradication (Howald et al. 2009). To minimize sparrow mortality, bait stations were used for 1 y in a 15-ha zone on West Anacapa in place of aerial baiting (Howald et al. 2009).

Mammals

Each of the eight California Channel Islands is home to an endemic subspecies of deer mouse *Peromyscus maniculatus* (Ashley and Wills 1987; Pergams et al. 2000). On Anacapa Island, *Peromyscus maniculatus anacapae* is found on all three islets; however, the species was suspected to be absent from East Anacapa from 1982 to 1997, likely as a result of invasive rats (Pergams et al. 2000). Pergams et al. (2000) determined that the deer mice on the three islets function as a single metapopulation, and using Population Viability Analysis they estimated that a breeding population of 1,000 mice would be sufficient to maintain metapopulation genetic structure. Based on this information, the mitigation plan of the rat eradication included captive holding, translocation of Middle and West Anacapa populations to East Anacapa, and subsequent reintroduction of populations to each islet (Howald et al. 2005; Gellerman 2007; Ozer et al. 2011). Santa Barbara Island is free of invasive mammals; therefore, we used the population of deer mouse on Santa Barbara Island, *Peromyscus maniculatus elusus*, as a control.

Intertidal community

The intertidal communities on Anacapa Island and at the southern end of Santa Cruz Island are characterized by a mix of taxa from both cold and warm regions, including gastropods (dominated by *Littorina* and *Lottia* spp.) and barnacles (*Chthamalus* and *Balanus* spp.; Blanchette et al. 2009). Few examples of black rat predation in the intertidal exist. Stapp (2002) found muscle tissue of mollusks (*Littorina* spp. and *Nucella* spp.) in the guts of rats collected nearshore on the Shiant Islands, Scotland. Carlton and Hodder (2003) identified three instances of black rats foraging directly in the intertidal (on Midway Atoll and at two locations in Chile) on 16 invertebrate and fish species, including crabs,



bivalves, gastropods, and fish. In addition, after the eradication of black rats on a small island near Oahu, Hawaii, researchers found an abundance of three intertidal invertebrate species that had been scarce prior to the eradication (Smith et al. 2006).

Methods

Sampling methods

Seabirds. Methods for monitoring Scripps's murrelet on Anacapa Island were reported by Whitworth et al. (2012, 2013). Briefly, nest monitoring for Scripps's murrelets was conducted in 10 sea caves, visited weekly to biweekly from March to August, 2001–2010 (Table 1). For each nest encountered they recorded whether 1) a clutch was laid, 2) the clutch hatched, and 3) the clutch was depredated by invasive rats or native deer mice (not distinguishable between the two). Similar control data were collected on Santa Barbara Island from 1993 to 2003 and 2007 to 2009 (Schwemm and Martin 2005; Harvey and Barnes 2009; Harvey et al. 2012). The same 10 sea caves were also searched for Cassin's auklet and ashy storm-petrel nests, along with 7 shoreline areas (Whitworth et al. 2015). However only the number of active nests (those with evidence of egg-laying) was documented for these species.

To monitor acoustic activity of ashy storm-petrels and Cassin's auklets, passive acoustic sensors were deployed at 11 locations in 2011: East (2), Middle (4), and West Anacapa (5); and 14 locations in 2012: Middle (3) and West Anacapa (11; Harvey et al. in press). Sensor deployment details, including recording schedules, are presented in Harvey et al. (in press). In addition, during sensor deployment, the area around the sensor was searched for Cassin's auklet and ashy storm-petrel nests and any nests were recorded (Harvey et al. in press). For each deployment location they calculated presence and absence of ashy storm-petrel or Cassin's auklet acoustic activity, and mean acoustic activity (mean calls per minute \pm SE).

Reptiles and amphibians. General monitoring methodology for the salamander and alligator lizard is outlined in Fellers et al. (1988). Briefly, the National Park Service conducted relative abundance surveys using cover-board transects during spring, pre-eradication (1993–1998 and 2000), and post-eradication (2003–2004 and 2010–2011; Table 1). Transects consisted of 30 or 60 permanent cover boards ($12 \times 12 \times 2$ in [$30.5 \times 30.5 \times 5$ cm]), with 1–4 transects sampled per islet (East, Middle, and West Anacapa) per sampling period. We calculated total rainfall by summing October through February rainfall prior to each spring survey from the closest weather station, Station 215: Channel Islands Harbor (VCWPD 2012).

Landbirds. To monitor rufous-crowned sparrows, Howald et al. (2009) conducted transect surveys 1 mo pre- and 1 mo post-eradication on West Anacapa (Table 1). In addition, they conducted wandering surveys and play-

back recordings post-eradication (2003–2005; Table 1). Separate post-eradication searches and playback recordings for rufous-crowned sparrows occurred on East and Middle Anacapa in March 2007, and on West Anacapa in March 2007, 2008, and 2011 in accessible locations (Hamilton 2007, 2008; McKown et al. 2013). In 2007, West Anacapa was only surveyed along the shoreline by boat. In 2011, researchers deployed 12 passive acoustic sensors across West Anacapa from March to September (McKown et al. 2013).

Mammals. National Park Service long-term deer mouse monitoring began in 1993 on East Anacapa and Santa Barbara islands and methods are presented in Fellers et al. (1988). Briefly, a capture–recapture study using standard Sherman live traps was used to sample mice within a square grid (10×10 traps). Traps were checked daily for a minimum of three nights during both spring and autumn seasons. These methods were expanded upon during 2000–2001, with trapping on two grids during spring through autumn seasons (Gellerman 2007). On East Anacapa, pre-eradication monitoring occurred during spring and autumn of 2000 and 2001 (Table 1; Gellerman 2007; Stanley 2012). Post-eradication monitoring was conducted during spring and autumn of 2010 and 2011 (Table 1; Stanley 2012). For comparison, we used the same spring and autumn sampling intervals for the control island, Santa Barbara (Stanley 2012). To evaluate genetic differentiation and variation after the captive holding and translocation of deer mice, Ozer et al. (2011) used microsatellite and mitochondrial DNA analyses. Ozer et al. (2011) obtained samples from all individuals held in captivity as well as samples from individuals captured during postreintroduction sampling on all three Anacapa islets (2003–2005).

Intertidal community. The National Park Service and the Partnership for Interdisciplinary Studies of Coastal Oceans visited two intertidal sites on West Anacapa, two sites on Middle Anacapa, and three sites on southern Santa Cruz Island (as a control) almost every autumn (4 y missing for Anacapa) and spring (2 y missing for Anacapa) from 1994 through 2010 (Table 1); Archived Material in PISCO Web; <http://data.piscoweb.org/DataCatalogAccess/DataCatalogAccess.html>). During each site visit, from three to nine photo quadrats were taken across four target zones (*Chthamalus* and *Balanus*, *Endocladia*, *Mytilus*, and *Silvetia*) spanning the entire intertidal. Photo quadrats measured 0.5×0.75 m and were scored by placing a 10×10 point grid over each photo (100 points total). The species under each point were recorded and then categorized into one of five groups (algae, sea grass, invertebrate, bare rock, or unknown) to determine percent cover for each photo-plot (Engle 2008).

Statistical analyses

Seabirds. We compared Scripps's murrelet data from Anacapa Island sea caves with data from Santa Barbara Island (as a control) to examine post-eradication changes



in 1) nest occupancy, 2) hatching success, and 3) depredation rates (Data S1). We only used data from years when both Anacapa and Santa Barbara islands were surveyed (2001–2002, 2007–2009). For all statistical results presented in this manuscript, we tested data to meet the assumptions of the statistical test and transformed data if necessary (JMP 10.0.0, SAS Institute Inc.). We arcsine-transformed the three data sets, calculated the annual difference between Anacapa and Santa Barbara islands, and used these values in two-sample *t*-tests to compare pre- vs. post-eradication time periods. We used an alpha level of 0.05 for significance in all analyses. As a result of the nature of the data collected, we conducted no statistical analyses for Cassin's auklet and ashly storm-petrel.

Reptiles and amphibians. For both the alligator lizard and slender salamander, we calculated the mean number of individuals per coverboard (Data S2). We used an analysis of covariance (ANCOVA) on mean slender salamander relative abundance (log-transformed) using eradication time period (pre- or post-eradication) as a factor, and rainfall as a cofactor. For the alligator lizard, we calculated mean number per coverboard using pre- and post-eradication spring survey data and used two sample *t*-tests on log-transformed data to compare the two time periods.

Landbirds. Pre-eradication quantitative data available for rufous-crowned sparrow were limited; therefore, we did not conduct any statistical analyses. Only observational data are reported in the results.

Mammals. We used deer mouse density estimates (mice/ha) for East Anacapa calculated by Stanley (2012) and Gellerman (2007; Data S3). To compare density estimates we combined the two data sets, log-transformed the data, and used a multifactor analysis of variance (ANOVA) with season (spring or autumn), island (Anacapa or Santa Barbara), and eradication time period (pre- or post-eradication) as factors. Details on genetic methods and data analyses are outlined in Ozer et al. (2011).

Intertidal community. We calculated mean percent cover for each group (algae, sea grass, invertebrate, bare rock, or unknown) for each year for both islands by aggregating photo-quadrat results across target zones and sites within years on each island. We log-transformed the annual mean values and used a multifactor ANOVA with season (spring or autumn), island (Anacapa or Santa Cruz), and eradication time period (pre- or post-eradication) as factors.

Results

Seabirds

Scripps's murrelet. We found a significant difference between pre- and post-eradication time periods for two of the three variables examined: proportion of eggs hatched/clutch (*t*-test, $t_{3,1} = -3.2547$, $P = 0.0237$) and rodent depredation rates on eggs ($t_{3,1} = 3.4301$, $P = 0.0208$). Although there was no significant difference in

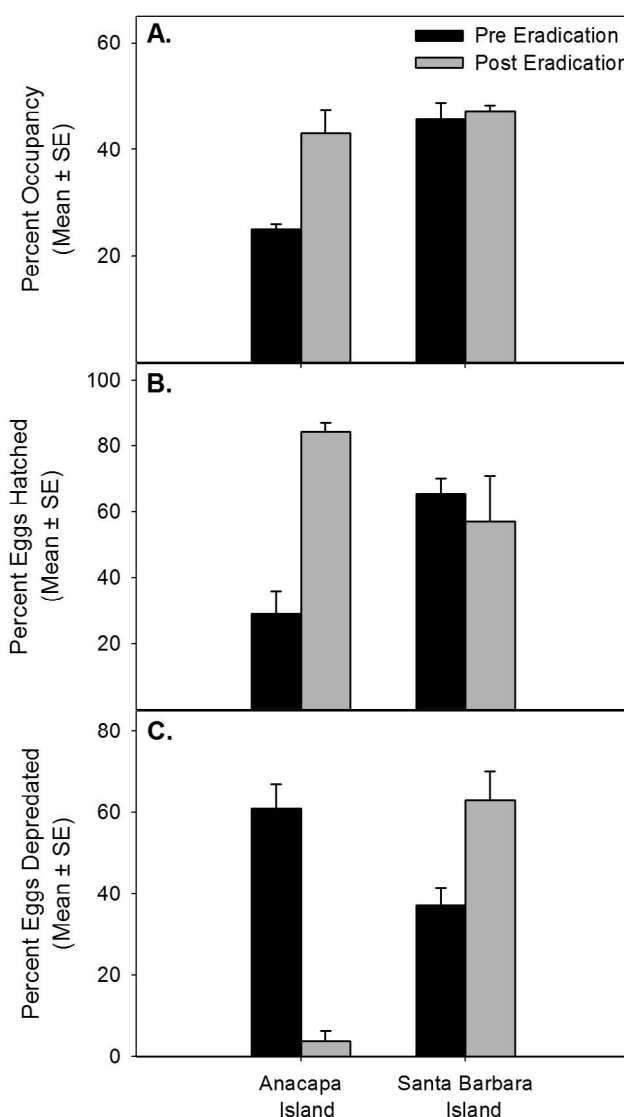


Figure 2. (A) Mean \pm SE (standard error) percent occupancy for Scripps's murrelets *Synthliboramphus scrippsi* breeding on Anacapa and Santa Barbara Islands, California pre- (black bars) vs. post- (grey bars) rat eradication. (B) Mean \pm SE (standard error) percent of eggs hatched for Scripps's murrelets *Synthliboramphus scrippsi* breeding on Anacapa and Santa Barbara Islands, California pre- (black bars) vs. post- (grey bars) rat eradication. (C) Mean \pm SE (standard error) percent of eggs depredated for Scripps's murrelets *Synthliboramphus scrippsi* breeding on Anacapa and Santa Barbara Islands, California pre- (black bars) vs. post- (grey bars) rat eradication. Data from Schwemm and Martin 2005; Harvey and Barnes 2009; Harvey et al. 2012; Whitworth et al. 2012.

percent occupancy, 191% more Scripps's murrelet eggs were hatching and 94% fewer nests were depredated on Anacapa Island post-eradication (Figure 2). These results indicate that, compared with the control island, there was a significant effect of the rat eradication on Scripps's murrelet breeding.

Cassin's auklet. No Cassin's auklet nests were found on Anacapa Island pre-eradication, with surveys dating back

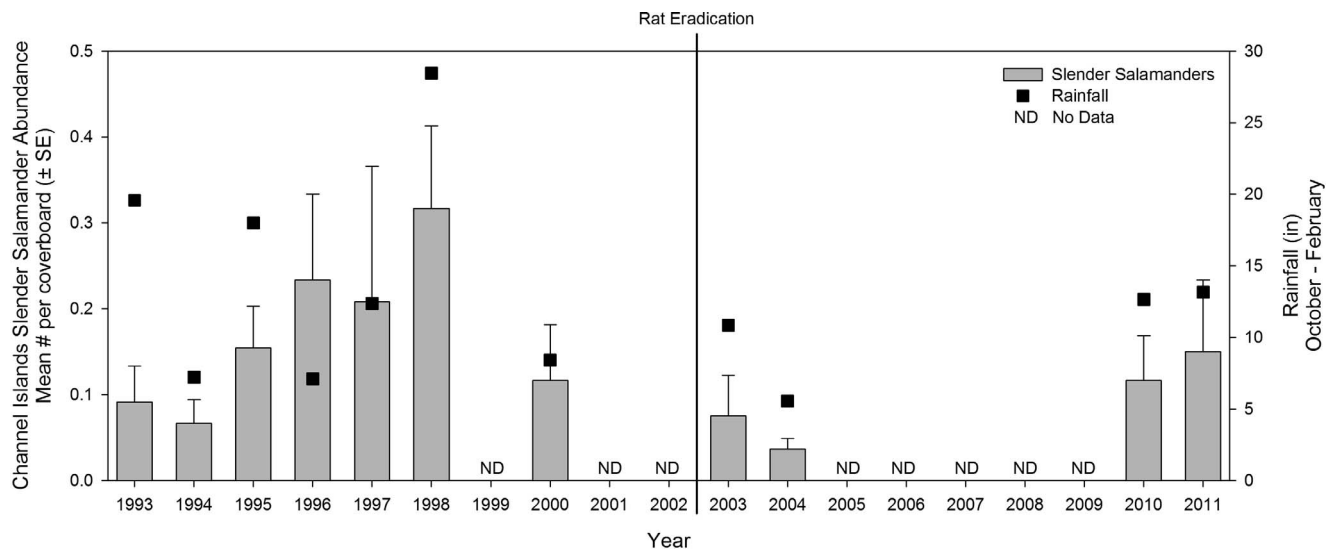


Figure 3. Mean \pm SE (standard error) Channel Islands slender salamander *Batrachoseps pacificus* spring survey abundance on Anacapa Island, California (grey bars; left axis). Rainfall (inches) occurring October through February prior to each spring survey is shown as black squares (right axis). Rat eradication completed in Autumn 2002 (solid vertical line). The abbreviation ND indicates no data were collected during that year.

to 1910 (Whitworth et al. 2015). Breeding Cassin's auklets (two nests) were found on Anacapa Island for the first time in 2003, post-eradication (Whitworth et al. 2005, 2015). Few if any nests were found between 2004 and 2008 (five total). In 2009, 11 Cassin's auklet nests were found and 3 of these nests contained eggs or chicks (Whitworth et al. 2012, 2015). Overall, post-eradication (2003–2012), Whitworth et al. (2015) found 42 nests in 6 shoreline areas, 17 of which were confirmed nests, and 25 were nests where breeding was inferred. Cassin's auklet vocal activity was detected by acoustic sensors at the same single survey site on West Anacapa during both 2011 and 2012 (Harvey et al. in press).

Ashy storm-petrel. No evidence of breeding ashy storm-petrels was found during sea cave searches pre- or post-eradication (2001–2010; Table 1) on Anacapa Island (Whitworth et al. 2012). In 2011, an acoustic sensor deployed on West Anacapa detected ashy storm-petrel vocal activity during June (0.09 ± 0.14 mean calls per min \pm SD; Harvey et al. in press). Researchers returned to this location in August and discovered an ashy storm-petrel nest with a chick in a rock crevice (Harvey et al. in press). Ashy storm-petrel vocal activity was detected at the same location in 2012 between 29 March and 24 July (0.06 ± 0.17 mean calls per min \pm SD; Harvey et al. in press). During both 2011 and 2012, no other ashy storm-petrel calls were detected at any other survey point by the acoustic sensors.

Reptiles and amphibians. For slender salamanders, our overall model was significant for pre- and post-eradication changes in relative abundance (ANCOVA, $r^2 = 0.19$, $F_{3,40} = 2.948$, $P = 0.044$) with fewer slender salamanders present post-eradication. However, examination of individual effects revealed that rainfall was an important, though marginally significant, cofactor ($F_{3,40} = 3.872$, $P =$

0.056), and removing rats did not significantly contribute to the variability in relative abundance of slender salamanders ($F_{3,40} = 3.478$, $P = 0.069$; Figure 3). We found no significant difference in mean number of alligator lizards/transect pre- vs. post-eradication on Anacapa Island, but power was low (0.26).

Landbirds. Transect surveys 1 mo post-eradication indicated a decline in rufous-crowned sparrows. Researchers detected 1.15 birds/transect pre-eradication (October and November 2002), and 0.47 birds/transect, or 59% fewer, post-eradication (Howald et al. 2009). During five surveys over the month following the eradication, researchers recorded only 11 rufous-crowned sparrows, and post-eradication wandering surveys on West Anacapa (2003–2005) were unsuccessful in locating any (Howald et al. 2009). In 2007, no rufous-crowned sparrows were found on any of the three Anacapa islets (East and Middle surveyed on foot, all three surveyed via boat), but six pairs and two individuals were found on nearby Santa Cruz Island (Hamilton 2007). In March 2008, two pairs responded to digital playback at the eastern end of West Anacapa (Hamilton 2008). In March 2011, opportunistic surveys counted seven rufous-crowned sparrows and acoustic sensors detected four rufous-crowned sparrow songs on West Anacapa (McKown et al. 2013).

Mammals. Within a year after reintroduction of deer mice, population sizes exceeded pre-eradication levels (Gellerman 2007). Although there was a 38% increase in relative abundance post-eradication, we found no significant difference in the interaction between islands and pre- and post-eradication time periods (Figure 4), indicating that the eradication had no effect on the population size of the deer mouse. However, upon examining individual effects, there was a significant

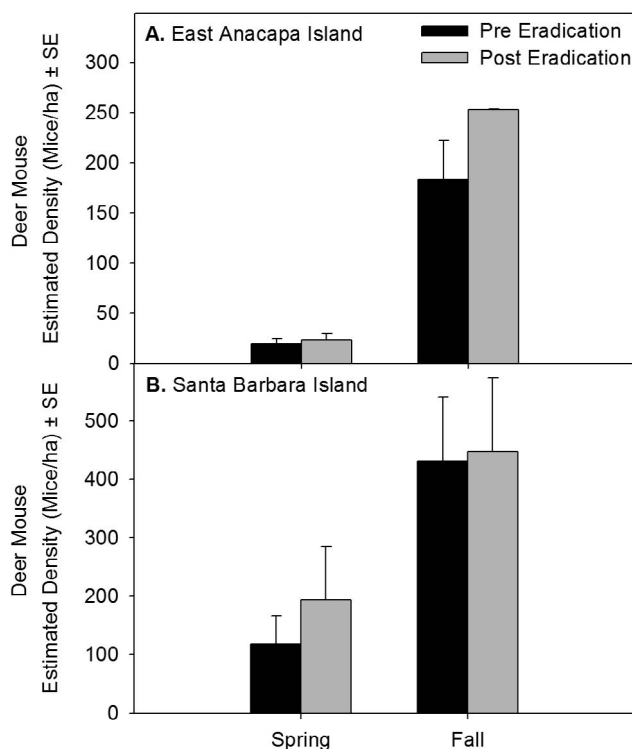


Figure 4. (A) Spring and autumn deer mouse *Peromyscus maniculatus anacapae* estimated density (mice/ha ± SE (standard error)) on East Anacapa Island, California pre- (black bars) vs. post- (grey bars) rat eradication. (B) Spring and autumn deer mouse *Peromyscus maniculatus anacapae* estimated density (mice/ha ± SE (standard error)) on Santa Barbara Island, California pre- (black bars) vs. post- (grey bars) rat eradication. Data from Stanley (2012) and Gellerman (2007).

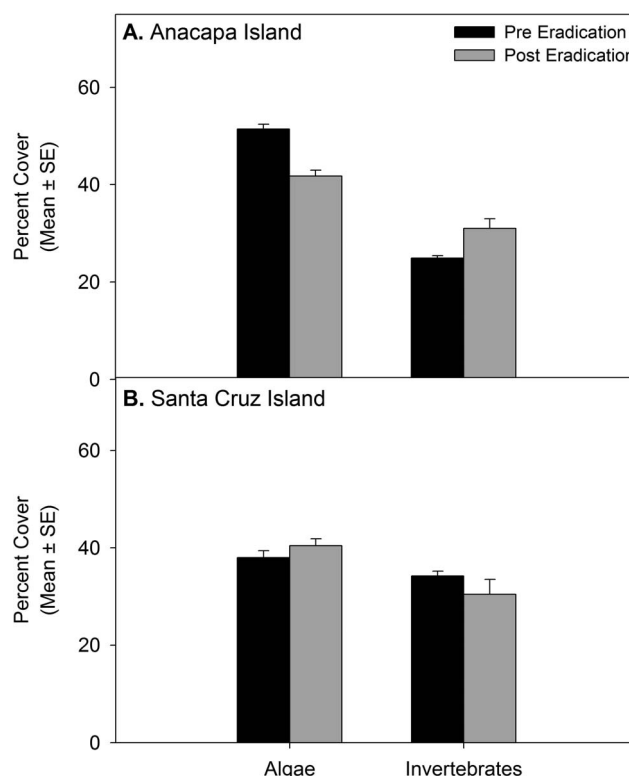


Figure 5. (A) Mean ± SE (standard error) percent cover of intertidal algae and invertebrates on Anacapa Island pre- (black bars) vs. post- (grey bars) rat eradication. (B) Mean ± SE (standard error) percent cover of intertidal algae and invertebrates on Santa Cruz Island pre- (black bars) vs. post- (grey bars) rat eradication.

Discussion

Our review of available data 10 y after the successful Anacapa Island rat eradication indicates that crevice and burrow-nesting seabirds (alcids and storm-petrels), intertidal invertebrate cover, and deer mice experienced either increases in numbers or a decrease in nest predation following rat eradication, while intertidal algal cover decreased. These increases are particularly noteworthy for the globally threatened Scripps's murrelets and ash storm-petrels that were the targeted beneficiaries of the eradication effort.

Howald et al. (2009) reported on short-term nontarget impacts of the eradication, and noted that rufous-crowned sparrows likely experienced significant mortality during the eradication. Assessing long-term recovery from this impact is not possible because of the limited survey effort prior to the eradication; the secretive nature of this species in steeper, less accessible habitat; and the species' concentration on parts of the island that are difficult to survey because of the presence of nesting brown pelicans *Pelecanus occidentalis* (a species easily disturbed by the presence of investigators; Collins 2008; Hamilton 2008). Nonetheless, this subspecies of rufous-crowned sparrow still persists on Anacapa Island, and predation from rats is no longer a potentially limiting factor (Collins 2008), suggesting this species should no

effect of season (ANOVA, $F_{1,1} = 10.588$, $P = 0.003$) with greater numbers of deer mice in the autumn, and also of island ($F_{1,1} = 6.715$, $P = 0.016$) with greater numbers of deer mice found on Santa Barbara Island. Overall these data support the hypothesis that the abundance of *Peromyscus* was not significantly negatively affected by the eradication. The deer mouse translocation successfully maintained genetic diversity of *P. maniculatus anacapae* across the islets, with no decrease in heterozygosity (Ozer et al. 2011). However, Ozer et al. (2011) found the East Anacapa population was less genetically differentiated because of translocation of deer mice from West and Middle Anacapa, and that some alleles were lost across all islets post-eradication.

Intertidal community. We found a significant interaction between island and pre- vs. post-eradication for both algal (ANOVA $F_{1,1} = 200.762$, $P < 0.0001$) and invertebrate ($F_{1,1} = 72.872$, $P < 0.0001$) cover, indicating that, compared with the control island, there was a significant effect of the eradication on both taxonomic groups. Algal cover decreased 18% while invertebrate cover increased 24% on Anacapa Island post-eradication (Figure 5). The control island, Santa Cruz, showed the opposite trend: algal cover increased 7% and invertebrate cover decreased 11%.

longer be limited by any short-term impacts from the eradication.

The intertidal community appears to have been directly affected by rat predation. After the eradication, invertebrate abundance increased, leading to an indirect decrease in intertidal algae cover due to increased herbivory in a classic “Green World” scenario (Hairston et al. 1960). The fact that we found the opposite trend on nearby rat-free Santa Cruz Island (decreased invertebrate abundance and increased algal abundance) supports the hypothesis that these changes were driven by the rat removal, and that rats were likely foraging directly on intertidal invertebrates. As the first study to specifically examine changes in the intertidal community following rat eradication, it will be interesting to understand these changes in more detail.

Although deer mouse populations on Anacapa experienced a bottleneck due to the eradication, post-eradication genetic analyses determined that genetically diverse populations of the Anacapa deer mouse subspecies were maintained. However, some distinct alleles present prior to eradication were lost, perhaps as a result of only a subset of reintroduced individuals reproducing or inaccuracies in the set of ecological and life-history population viability analysis input parameters used in pre-eradication genetic diversity models (Ozer et al. 2011). There was also a reduction in the genetic differentiation (change in allele frequency) of the East Anacapa deer mouse population compared with the Middle and West populations; likely due to the translocation of populations from Middle and West Anacapa to East Anacapa as part of the nontarget mitigation. This was not anticipated because pre-eradication evaluation of the genetic diversity of deer mice across the three islets indicated that the populations are genetically similar, suggesting that translocation as a mitigation to sustain the Anacapa deer mouse populations would not significantly affect gene diversity (NPS 2000; Pergams et al. 2000). Nonetheless, from a population perspective, post-eradication relative abundances of deer mice were not significantly different than pre-eradication abundances, indicating that the translocation and reintroduction was successful in maintaining viable populations and the ecological functions of Anacapa deer mice. Collectively, these results illustrate the complexity of trade-offs that may need to be assessed for eradications that have the potential to significantly impact nontarget native populations.

We found no significant change in herpetofauna (alligator lizard and slender salamander) populations 10 y post-eradication. The lack of response by the alligator lizard and slender salamander to the eradication, as indicated by our analysis, is difficult to interpret because of the paucity and high variability of survey data and the absence of control populations for these species. Reptiles and amphibians are known to be vulnerable to black rats and are expected beneficiaries from rodent eradication (Towns et al. 2006). Likewise, insufficient long-term data on landbird populations precluded a quantitative assessment of their response to rat eradication. Evidence of the continued presence of all landbird

species (including raptors) that were observed on the island pre-eradication indicates limited long-term negative impacts. Unfortunately, there were no data to test for changes in terrestrial plant and terrestrial invertebrate communities.

Collectively, changes we observed in marine vertebrates (seabirds), terrestrial vertebrates (native deer mice), and intertidal invertebrates and algae are consistent with mechanisms that have been discussed in previous short-term studies examining the ecosystem benefits of invasive rat removal (e.g., Navarrete and Castilla 1993; Gellerman 2007; Jones et al. 2008; Kurlle et al. 2008). They support the hypothesis that invasive rats have a multitude of direct and indirect effects that reverberate throughout insular ecosystems, and that rat removal can result in both rapid benefits and additional long-term and indirect changes. Our results are relevant to rat eradications on other islands in Mediterranean woodland and scrub biomes and are consistent with results reported for islands in boreal forest taiga, temperate coniferous forest, desert and xeric shrubland, and several tropical and temperate biomes (Major and Jones 2003; Pascal et al. 2005; Fukami et al. 2006; Smith et al. 2006; Jones et al. 2008; Meyer and Butaud 2009; Mulder et al. 2009; Traveset et al. 2009). Although the effects of the different *Rattus* spp. vary, they are pervasive enough that island species’ (with their unique behavioral, morphological, and life history vulnerabilities) response to rat eradication is likely consistent across a large range of habitats (Towns et al. 2006).

Our results demonstrate the benefits of the Anacapa Island rat eradication. In particular, they demonstrate that significant recovery of affected species can occur through passive restoration (i.e., without management intervention to promote post-eradication recovery). Although no additional post-eradication monitoring on Anacapa Island will occur, in the future, more consistent inclusion of control populations, more robust survey effort and design to measure direct and indirect effects, and the inclusion of terrestrial plants and invertebrates, would greatly increase our ability to predict the outcomes of rat eradications on islands world-wide. Improved monitoring of eradication outcomes will help island managers anticipate both potential detrimental impacts and biodiversity benefits resulting from rat eradications, as documented recently on Hawadax Island, Alaska (Croll et al. 2016).

Supplemental Material

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Data S1. Data on the percent hatched, percent occupancy, and percent depredated Scripps’ Murrelet nests on Anacapa Island (ANI) and Santa Barbara Island (SBI) are contained in a Microsoft Excel file titled DataS1_Newton_Seabirds.xlsx. Column headings include Eradication Time Period, Year, %Hatched_ANI,



%Hatched_SBI, %Occupancy_ANI, %Occupancy_SBI, %Depredated_ANI, and %Depredated_SBI.

Found at DOI: <http://dx.doi.org/10.5061/10.3996/082015-JFWM-073.S1> (11 KB XLSX).

Data S2. Data on the number of Channel Islands slender salamanders (SLSA) and southern alligator lizards (ALLI) per coverboard over the sampling period along with the total amount of rainfall (in inches) occurring October through February prior to each spring survey are contained in a Microsoft Excel file titled Data-S2_Newton_Reprtiles_Amphibians.xlsx. Column headings include Eradication Time Period, Year, Season, Islet, Transect, # coverboards, # SLSA per coverboard, # ALLI per coverboard, and Oct – Feb Rainfall (in).

Found at DOI: <http://dx.doi.org/10.5061/10.3996/082015-JFWM-073.S2> (11 KB XLSX).

Data S3. Data on the mean number of deer mice per hectare on East Anacapa Island (EAI) and Santa Barbara Island (SBI) are contained in a Microsoft Excel file titled DataS3_Newton_Mammals.xlsx. Column headings include Eradication Time Period, Year, Season, Mean_Mice_EAI, Mean_Mice_SBI.

Found at DOI: <http://dx.doi.org/10.5061/10.3996/082015-JFWM-073.S3> (11 KB XLSX).

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