

available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/biocon

Experimental control of a native predator may improve breeding success of a threatened seabird in the California Channel Islands

Sarah A. Millus^a, Paul Stapp^{a,*}, Paige Martin^{b,1}

^aDepartment of Biological Science, California State University Fullerton, Fullerton, CA 92834-6850, USA

^bNational Park Service, Channel Islands National Park, 1901 Spinnaker Drive, Ventura, CA 93001, USA

ARTICLE INFO

Article history:

Received 26 September 2006

Received in revised form

24 May 2007

Accepted 27 May 2007

Available online 12 July 2007

Keywords:

Peromyscus maniculatus

Predator control

Seabirds

Xantus's Murrelet

ABSTRACT

Predation by native deer mice (*Peromyscus maniculatus elusus*) is considered the greatest threat to nest success of Xantus's Murrelet (*Synthliboramphus hypoleucus scrippsi*), a small, crevice-nesting seabird, on Santa Barbara Island, where about half of the known US population breeds. Reduction of mouse predation has been proposed as one way to increase reproductive success on Santa Barbara Island, California. Between February and June 2004, approximately 1650 mice were translocated from the largest and most consistently monitored murrelet colony on the island, reducing mouse population density significantly relative to a control site. During the translocation period, significantly fewer eggs were preyed upon by mice (20.5%) than the average (36.7%) between 1993 and 2005, excluding 2004. Productivity in 2004 (1.11 eggs hatched nest⁻¹) was also significantly higher than the 12-year average (0.93 eggs hatched nest⁻¹). More eggs were laid and hatched in 2004 than in most previous years, but overall, hatching success was not markedly higher, in part because other reasons for nest failure, e.g., abandonment, egg mortality, were important in 2004. Although local mouse removals may effectively reduce egg predation on a limited scale, particularly during periods when risk may be higher because alternative prey for mice are scarce, island-wide eradication of mice is not practical or desirable here because of the mouse's endemic status. Because a combination of other terrestrial and at-sea factors are known to influence population viability of Xantus's Murrelet, conservation strategies that incorporate intensive efforts both on land and at sea will likely be the most effective.

© 2007 Elsevier Ltd. All rights reserved.

1. Introduction

Many seabirds preferentially nest on islands that lack mammalian predators (Gaston, 2004), and few seabird species are adapted to avoid ground predators (Furness and Monaghan, 1987). Most studies of the effects of predators on seabirds have focused on introduced species (see Moors and Atkinson,

1984), such as rats *Rattus* spp. (e.g., Hobson et al., 1999; Martin et al., 2000; Stapp, 2002), feral cats *Felis catus* (Kirkpatrick and Rauzon, 1986; Martínez-Gómez and Jacobsen, 2004), foxes *Vulpes vulpes* (Norman, 1971), and mink *Mustela vison* (Nordström et al., 2003). Predation by native species has received less attention (Murray et al., 1983; Blight et al., 1999; Drever et al., 2000; Bradley and Marzluff, 2003), but these species

* Corresponding author. Tel.: +1 714 278 2849; fax: +1 714 278 3426.

E-mail address: pstapp@fullerton.edu (P. Stapp).

¹ Present address: 929 Hollister Ave, Lehigh Acres, FL 33936.

0006-3207/\$ - see front matter © 2007 Elsevier Ltd. All rights reserved.

doi:10.1016/j.biocon.2007.05.017

can have a considerable impact on seabird populations, especially when mortality is compounded by other population threats, such as habitat destruction, over-fishing of prey and oil pollution (Evans, 1984). In light of these more recent, anthropogenic factors, mortality from native predators may now pose a real threat to the long-term persistence of some seabird populations.

Xantus's Murrelet (*Synthliboramphus hypoleucus*) is a small, crevice-nesting alcid that breeds exclusively on islands off the coast of southern California and northwestern Baja California. Globally, the breeding population is estimated to be 17,900 individuals (Karnovsky et al., 2005). The largest breeding population of Xantus's Murrelet in the United States is located off the coast of southern California on Santa Barbara Island (SBI). Approximately 1500 breeding pairs, representing about half of the known US population, nest on this island, mainly in crevices and to a lesser extent under shrubs (Burkett et al., 2003). Historically, murrelet numbers on SBI had been reduced by the introduction of exotic species in the early 1900s: feral cats preyed on chicks and adults, whereas rabbits and sheep destroyed native shrub vegetation which provided nesting habitat for murrelets and other seabirds. The replacement of native grasslands and shrublands by exotic grasslands as a result of agriculture and disturbance dramatically changed the structure of the vegetation and may have altered food availability for nest predators (Murray et al., 1983). Although the last exotic vertebrates were eradicated from SBI in 1981 (Halvorson et al., 1992), surveys of the nesting population of Xantus's Murrelet on SBI suggested that the population continued to decline between 1977 and 1991 at an estimated rate between 2.5% and 5.3% per year (Carter et al., 1992; Sydeman et al., 1998), which contributed to the decision to list the species as Threatened by the State of California (Burkett et al., 2003; Carter et al., 2005). Factors that may have contributed to this decline at SBI include, in order of importance: relatively high levels of egg predation by deer mice; relatively high adult predation by avian predators; changes in prey availability; loss of nesting habitat; artificial light pollution; and other anthropogenic mortality at sea (Carter et al., 1992, 2000; Burkett et al., 2003; Roth et al., 2005). However, because at-sea risks are difficult to quantify and control, conservation efforts have focused on increasing survival of breeding birds and their young on land, especially on SBI.

The most important source of mortality for breeding murrelets on SBI is predation by other native species. Adults are killed by Barn Owls (*Tyto alba*) and Peregrine Falcons (*Falco peregrinus*), whereas most egg mortality is attributed to endemic deer mice *Peromyscus maniculatus elusus* Nelson and Goldman (Murray et al., 1983; Drost and Lewis, 1995; Sydeman et al., 1998; Pacific Seabird Group, 2002a,b). Egg predation is considered to have a great impact on murrelet populations on SBI, with estimates of egg loss ranging from 19% to 64% each year (Sydeman et al., 1998; Schwemm and Martin, 2005). Using population viability analysis, Sydeman et al. (1998) concluded that increasing adult survival alone would be insufficient to stem the recent population decline, and argued that elimination of, or at least significant (26–61%) reduction in, predation by mice on eggs would be necessary to achieve a stable population. Since 1995, resource managers have debated non-lethal removal of mice from fenced murrelet nesting areas

to create 'mouse-free' areas, or reduction of avian predators such as owls over large island areas as strategies to improve reproductive success on SBI. Several studies have shown that predator control can increase hatching success and post-breeding population sizes of birds (e.g., Côté and Sutherland, 1997; Guillemette and Brousseau, 2001; Moorhouse et al., 2003; Nordström et al., 2003). For example, black rats (*Rattus rattus*) were completely eradicated from Anacapa Island in November 2002, another island in the region where murrelets breed. Eradication has made a difference: nest predation was significantly reduced, and more new nest sites have become occupied than before eradication (Jones et al., 2005; Whitworth et al., 2005).

Because eradication is not an appropriate goal for control of native endemic predators, alternative methods of control that protect the species of concern while safeguarding the persistence of the predator must be considered. Several control methods have been used to remove or exclude predators from bird nesting areas, including trapping (Moorhouse et al., 2003; Nordström et al., 2003; Seymour et al., 2005), poisoning (Jones et al., 2005) and fencing (Mayer and Ryan, 1991; Morris et al., 1992; Keedwell et al., 2002). As part of a broader study of interactions between seabirds and mice on SBI (Millus, 2006), we examined the efficacy of controlling deer mice at murrelet colonies during the nesting season as a means of reducing rates of nest predation and improving murrelet reproductive success. Mice were live-trapped and translocated from the largest murrelet colony on SBI throughout the murrelet breeding season in 2004. A reduction of mouse abundance was expected to decrease the proportion of murrelet eggs broken by mice compared to historical rates of egg loss, and result in an increase in murrelet productivity. To assess the feasibility of using mouse control as a conservation tool, the work effort required to conduct the mouse translocations was also evaluated.

2. Materials and methods

2.1. Study area

Santa Barbara Island (33° 28'N, 119° 2'W) is the smallest of the California Channel Islands, measuring only 2.6 km². It is located 64 km southwest of Los Angeles and 39 km west of Santa Catalina Island, and is one of five islands that comprise Channel Islands National Park (CINP). The climate is Mediterranean, with a mild wet season from October to April and a long dry season. Its coastline is characterized by steep, sloping rocky cliffs, with a few small, rocky beaches. There are isolated, extensive patches of native giant coreopsis (*Coreopsis gigantea*) and prickly pear (*Opuntia littoralis*) on sea slopes. The interior of the island is dominated by non-native plants, mostly grasses such as oats (*Avena* spp.), brome (*Bromus* spp.) and barley (*Hordeum* spp.), which are remnants of farming and ranching that occurred on the island in the early 20th century, and crystalline iceplant (*Mesembryanthemum crystallinum*), which was introduced in the late 19th century (Philbrick, 1972). Deer mice are the only terrestrial, non-volant mammals on SBI and have been present on the Channel Islands as early as 500,000 years ago (Ashely and Wills, 1987).

The largest murrelet monitoring plot on SBI is located at the south end of the island, on the sloping sea cliffs of Cat Canyon (Fig. 1). This area is characterized by rocky outcrops and sparse vegetation, mostly buckwheat (*Eriogonum giganteum*), boxthorn (*Lycium californium*) and cholla (*Opuntia prolifera*). The Cat Canyon murrelet monitoring plot includes 78 known nest sites, +63 potential nest sites and crevices, that are monitored annually by CINP staff as part of the National Park Service (NPS) Seabird Monitoring Program. A second, smaller murrelet monitoring plot (Nature Trail; 60 monitored sites) is located on the eastern side of the island, near the NPS ranger station. This area is also rocky and steep, but the dominant shrub is silverlace (*Eriophyllum nevinii*).

Adult murrelets spend most of their lives at sea and come to land between the months of March and June to breed. Except for incubation, murrelets restrict their activity on land to the hours between dusk and dawn (Murray et al., 1983). *Synthliboramphus* murrelets are unique among alcids in that they typically lay two, relatively large eggs, the first of which is left unattended for approximately 8 d; eggs are also occasionally left unattended between incubation shifts, the duration of which is influenced by the availability of marine prey for parents (Murray et al., 1983; Roth et al., 2005). Approximately 44% of egg mortality in 1975–1977 was attributed to mouse predation on neglected eggs (Murray et al., 1983).

As part of the CINP Seabird Monitoring Program, known and potential murrelet nests were checked approximately every 5 d to determine the breeding status of murrelets and the status of eggs and chicks. In 2004, nests were checked between March 1 and June 21. Eggs broken by mice are characterized by a shiny membrane adhering to the inside surface of the eggs, with remains of yolk. Conspicuous bite marks are often present. In contrast, hatched eggs lack the shiny membrane or yolk and have smoother edges (Sydeman et al., 1998). Other possible egg fates included disappeared (egg observed

but disappeared without sign of predation or abandonment), abandoned (egg left unattended by adult for >3 nest checks), addled (appropriate incubation length, but egg not viable), and unknown.

CINP biologists estimate two parameters related to mouse predation on eggs. Measured predation is calculated as the number of observed broken eggs believed to be eaten by mice, and includes eggs that are abandoned or otherwise broken, and then subsequently scavenged by mice. Assumed predation is calculated as the number of observed eggs believed to be eaten by mice (i.e., measured predation), plus the number of disappeared eggs. Disappeared eggs can be lost for reasons other than mice; 10% and 14% of eggs disappeared in 2003 and 2004, respectively, on the San Benito Islands, where mice are absent (Wolf et al., 2005). Measures of predation therefore include some eggs that are lost for reasons other than mouse predation. However, the majority of observed eggs attributed to mouse predation or disappearance are assumed to be viable otherwise. We used estimates of assumed predation as our measure of mouse egg predation because it includes all lost eggs that were broken by mice. We combined all other fates to describe rates of egg failure for reasons other than predation. Besides predation, abandoned and addled eggs are the most common types of failed eggs.

2.2. Experimental mouse removals

In February 2004, a reduction trapping grid was established at the Cat Canyon murrelet monitoring site (Fig. 2). The grid was 70 × 40 m, with a total of 28 trapping stations (two small Sherman live traps per station, for a total of 56 traps). The steep, rocky terrain and the presence of nesting California Brown Pelicans (*Pelecanus occidentalis californicus*) nearby limited the extent of the grid, but 70% of murrelet nests active in 2004 were within 30 m of the removal grid. A reduction control grid

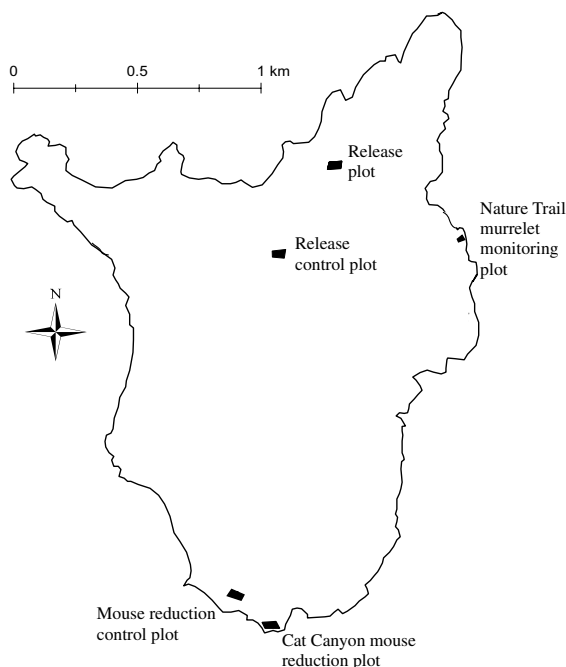


Fig. 1 – Map of Santa Barbara Island showing location of mouse trapping grids for 2004 (black polygons).

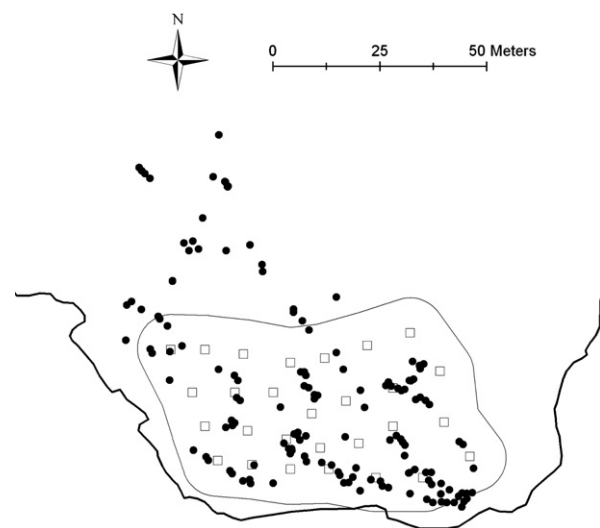


Fig. 2 – Location of mouse translocation grid (squares; 2 traps/station) and murrelet nests (circles) at Cat Canyon on SBI. Dashed line represents 8 m buffer surrounding the trapping grid, reflecting the approximate maximum distance moved by mice during trapping sessions (Millus, 2006).

was located on the same slope but outside the murrelet nesting area, ~200 m west of the removal site, with vegetation and substrate characteristics similar to the reduction grid (Fig. 1). This area contained no murrelet nests, and this grid was established to measure differences in mouse abundance between the mouse reduction grid and a similar area where mice abundance was not manipulated. A mouse release grid was established at the northern end of the island, approximately 2 km from the reduction site. This grid was set in a small patch of *Coreopsis* and buckwheat surrounded by grassland. A control grid for the release site was established ~450 m southwest of the release grid in a large isolated patch dominated by *Coreopsis*, prickly pear and buckwheat. The release grid, release control and reduction control grids all measured 60 × 40 m. Trapping on control grids provided a reference for changes in mouse abundance due to our translocations. Extensive nesting by pelicans prevented us from using the only other accessible murrelet monitoring plot on SBI (Nature Trail) as a control.

Beginning 28 February 2004, mice were trapped at the reduction grid and transported to the release grid. Mice captured on the reduction grid were left in their traps, which were placed in a wooden box on a frame pack, and then carried to the release grid. Mice were ear-tagged, measured, classified by age, sex and breeding condition, and then released. National Environmental Protection Agency (NEPA) and NPS regulations required that mice be transplanted rather than euthanized. Translocations of mice from the monitoring grid took place during roughly 2-wk periods, followed by a 1-wk break, resulting in translocations occurring about 3 wk out of each complete month of trapping. Translocations were conducted on the mornings of 28 February–1 March, 11–17 March, 25 March–4 April, 14–19 April, 23 April, 25 April, 26 April, 28 April, 1 May, 3 May, 5–10 May, 12 May, 14–16 May, 27–29 May, 31 May and 2 June 2004.

Reduction, reduction control, and release sites were trapped prior to the initiation of mouse control in mid-February and March. The removal control was also trapped 6–8 May and 5–7 June. The release site was trapped approximately every 3 wk (3–5 April, 26–28 April, 16–18 May, 6–8 June and 25–27 June). The release control was trapped 10–12 March, 18–20 April, 12–14 May, 30 May–1 June and 21–23 June. All field handling and marking procedures were approved by the Institutional Animal Care and Use Committee at California State University at Fullerton, and with permits from California Department of Fish and Game and NPS.

2.3. Data analysis

Statistical analyses were performed using SAS version 9.0. Densities were not calculated for the reduction grid because mice were continually removed from this site. Instead, changes in capture success were used to assess differences in mouse abundance on the reduction grid compared to control sites. For the mouse reduction grid, daily capture success was calculated as the proportion of mice captured each night per number of available traps × 100% (mice 100 TN⁻¹; TN = trap-nights, adjusted for the number of sprung but empty traps). For control grids trapped for 3 consecutive nights, average daily capture success was calculated as the

average proportion of mice captured per number of available traps during 3 nights of trapping × 100%. Mouse densities were calculated using the CAPTURE algorithms (Otis et al., 1978) implemented in Program DENSITY (Efford, 2004).

Because we were unable to monitor murrelet nesting or mouse abundance at the Nature Trail colony, different criteria were required to evaluate success of reducing mouse abundance for improving murrelet reproductive success. Historical rates of egg predation by mice, collected by CINP biologists from 1993 to 2005, were used to compare to estimates of assumed predation in 2004 during mouse removals. Information on murrelet nest success has been collected by CINP on SBI since 1983, but data have only been collected on a regular basis using more standardized protocols with more frequent nest visits since 1993; therefore, only these latter data were used in our analyses. We set as our criteria for success a reduction in nest predation below the 95% confidence limits of the mean value of nest predation between 1993 and 2005, excluding 2004 (36.7%; 95%CI: 26.6–46.8, $n = 12$), and an increase in productivity (eggs hatched per nest) above the 95% confidence limits for the 1993–2005 mean, again excluding 2004 (0.93; 95%CI: 0.78–1.09; calculated from Schwemm and Martin, 2005 and P. Martin, unpublished data).

3. Results

Prior to deer mouse removals in early February, mouse abundance was high on the reduction (murrelet monitoring plot), reduction control and release sites (Table 1). Estimated mouse population density was slightly lower on the reduction site than on the control site in February 2004, but confidence limits of estimates overlapped, except for the release control. However, the control grid was trapped almost a month after the others, which may also partially explain why abundance was higher on this site. During 47 d of mouse removals between February and June, a total of 1652 individual mice (1684 captures) were translocated from the Cat Canyon removal grid to the release grid ~2 km away. Only eight mice (<1% of captures) were recaptured on the colony grid, an average of 12 d (range: 1–34 d) after their initial capture. One mouse, an adult female, was captured 3 d after her initial capture, and 1 d after her second capture. Juveniles consistently made up a small proportion of captures (11%), especially during April. Mouse breeding peaked by late April, and remained high through May and early June. No mice in breeding condition were captured after early June.

Daily capture rates on the mouse removal grid varied greatly (Fig. 3). Capture success was high on control sites throughout the entire season, with 90–109% average daily capture success and an average density of 326 individuals ha⁻¹ (range: 223–444 mice ha⁻¹). There were no significant differences in mouse abundance among control grids over time during the removal period (February–June), either when considering mouse capture success (repeated-measures ANOVA, $F = 2.93$, $df = 3,4$, $P = 0.163$) or mouse density ($F = 2.90$, $df = 3,4$, $P = 0.165$). The average daily capture rate for the entire removal period on the removal grid (64.75 ± 3.9 mice 100 TN⁻¹; $\bar{X} \pm 1$ SE; $n = 47$ nights) was significantly lower than the average daily capture rate for the control grids (99.11 ± 1.7 mice 100 TN⁻¹; $\bar{X} \pm 1$ SE; $n = 18$; Wilcoxon rank-sums test,

Table 1 – Mouse densities and associated capture results for all trapping sites except removal site on SBI in 2004

Start date	Site	Total individuals	Total captures	Model used	$\hat{N} \pm 95\%CI$	Mean maximum distance moved (m)	Density (mice ha ⁻¹)	SE (\hat{D})
12-February	Removal	87	156	Mo	96 ± 4	11.4	257	25
14-February	Removal Cntrl	82	143	Mo	92 ± 4	7.4	323	29
15-February	Release	82	132	Mo	98 ± 6	5.9	384	39
10-March	Release Cntrl	98	153	Mo	121 ± 8	6.8	444	42
18-April	Release Cntrl	80	142	Mo	88 ± 4	6.3	335	29
6-May	Removal Cntrl	65	129	Mo	68 ± 2	8.3	223	19
12-May	Release Cntrl	85	138	Mo	101 ± 6	5.5	409	39
30-May	Release Cntrl	80	138	Mo	90 ± 5	8.1	300	30
5-June	Removal Cntrl	69	141	Mo	71 ± 2	7.6	245	19
18-June	Removal	66	144	Mo	67 ± 1	11.1	183	14
21-June	Release Cntrl	97	152	Mo	119 ± 8	7.5	415	46

Estimates generated using CAPTURE in DENSITY (Efford, 2004). 'Removal' data is for removal grid trapping before and after removals took place.

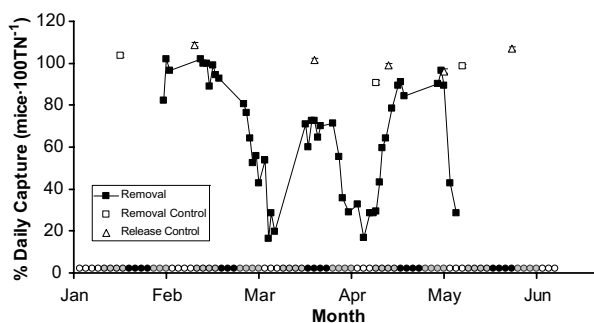


Fig. 3 – Daily capture rate of deer mice on reduction and control grids during the experimental reduction of mice from February to June 2004 on the Cat Canyon murrelet colony on SBI. Circles at the bottom of the figure represent different lunar phases, with open and filled symbols indicating full and new moon periods, respectively.

$U = 943$, $P < 0.0001$). As expected, more mice (~15% on average) were removed from the 18 stations along the edges of the grid than the interior 10 stations ($\bar{X}^2 = 7.37$, $P = 0.007$), but large numbers of mice were removed from all trap stations ($\bar{X} = 60$, $SD = 9$, range = 41–80; $n = 28$ stations).

Patterns of variation in capture success on the removal grid suggested that mouse activity was affected by moonlight intensity (Fig. 3). To assess this, moon age, which assigns one phase of the moon (new, first and last quarters and full) to each day of a month, was used to approximate the intensity of moonlight on a given night of trapping. Mouse capture success on the removal grid was highest during new moon and lowest during full moon ($F = 7.35$, $df = 1.44$, $P = 0.010$). There was no relationship between moon age and capture success on the control grids ($F = 2.00$, $df = 1.14$, $P = 0.179$), in part because the number of mice captured was consistently so high. The effect of removals on mouse abundance, however, could not be attributed solely to moonlight effects. Capture success was significantly lower on the removal grid during periods of low moonlight (new, first, and last quarters) compared to control grids during the same moon phases ($t = 2.19$, $df = 42$, $P = 0.034$).

During the February–June removal period, 15 murrelet eggs from 11 nests, or 20.5% of known eggs laid, were assumed to be

eaten by mice, a rate that was significantly below the 95% confidence limits of the 1993–2005 mean (36.7%) for the Cat Canyon colony (Fig. 4a). As a consequence, estimated nest productivity (1.11 eggs hatched nest⁻¹) was significantly higher than the 12-year average (0.93 eggs hatched nest⁻¹; Table 2). The proportion of egg failures that were attributed to predation reached its lowest value in 2004 (46.9%) over the entire 12-year period, and was well below the 95% confidence interval for the 1993–2003, 2005 mean (77.6%; Fig. 4b). Eleven eggs were abandoned and three eggs were added in 2004 (77% of non-predation related egg failures; 18% of all eggs laid), which was only slightly fewer than the number of eggs estimated to have been

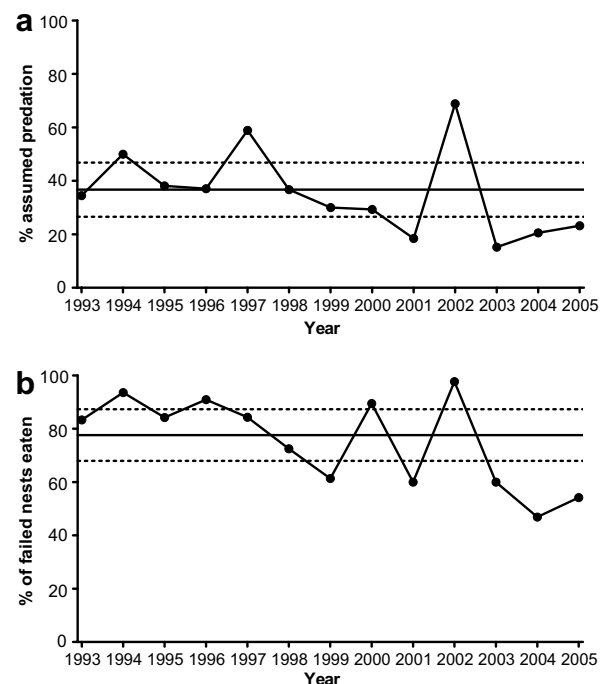


Fig. 4 – Rates of (a) assumed predation on Xantus's Murrelet eggs and (b) proportion of failed eggs that were attributed to predation between 1993 and 2005, including during the mouse-removal experiment in 2004. Solid lines are mean values between 1993 and 2005, excluding 2004, with dashed lines denoting 95% confidence intervals.

Table 2 – Nest success of Xantus's Murrelet at the Cat Canyon colony on SBI between 1993 and 2005, including 2004, the year of experimental mouse removals

Variable	Year													\bar{X} (95% CI) (1993–2003, 2005)
	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	
Nests occupied	41	38	30	33	36	36	45	33	35	31	46	37	37	36.7 (33.5, 40.0)
Nests attempted	42	42	30	34	48	47	53	35	38	44	50	45	40	41.9 (37.5, 46.3)
Eggs laid	58	58	42	54	73	79	90	58	65	61	79	73	56	64.4 (55.9, 72.9)
Eggs hatched	34	27	23	32	22	39	46	39	45	18	59	41	32	36.7 (27.2, 42.1)
Hatching success	58.6	46.5	54.8	59.3	30.1	49.4	51.1	67.2	69.2	29.5	74.7	56.2	57.1	53.9 (45.0, 62.9)
Productivity/nest	0.83	0.71	0.77	0.97	0.61	1.08	1.02	1.18	1.29	0.58	1.28	1.11*	0.86	0.93 (0.78, 1.09)

Asterisk denotes 2004 values that were outside of 95% confidence limits (95%CI) for the 1993–2005 mean, excluding 2004. Historical data from Schwemm and Martin (2005) and P. Martin, unpublished data.

eaten by mice (15). Of all failed eggs, 34% were abandoned and 9% were added. Relatively large numbers of eggs were laid and hatched in 2004, but hatching success (56.2%; Table 2) was not unusually high, in part because of the large number of eggs that were found abandoned and added.

Rates of nest predation in the Cat Canyon colony seemed to have declined over the past 57 years, with the exception of 2002 (Fig. 4). If 2002 is considered an outlier and omitted, the estimated nest predation rate in 2004 (20.5%) was still well below the lower 95% confidence limit (25.1%) for 1993–2005 (\bar{X} = 33.8%), and the 2004 estimate of productivity (1.11 eggs hatched nest⁻¹) was just inside the 95% confidence limit (1.12 eggs hatched nest⁻¹) of the mean from 1993 to 2005 (0.96 eggs hatched nest⁻¹). Moreover, our estimate of nest predation in 2004 was also below the 95% confidence limits of mean nest predation rate for years that, like 2004, had relatively dry winters (\bar{X} = 43.0%, 95%CI = 14.6, n = 5). We note that low rates of egg predation and high murrelet productivity have also been observed in some previous years (Table 2, Fig. 4a).

Because of interest in the feasibility of implementing mouse removals, we estimated the amount of effort required to conduct the removal experiment. A total of 289 h over the entire 2004 season were spent on mouse removals, in addition to approximately 54 h of travel between SBI and the mainland. The average time spent each day on mouse removals over a 47-d period was approximately 4.5 person h, which includes checking and setting traps, on-island travel time, and mouse processing time. Each day, approximately 1.25 h were spent on travel between grids, 45 min on either collecting or setting traps and 2 h on processing and releasing mice. Approximately 10 km of walking was required each day, for a total of 470 km hiked.

4. Discussion and conclusions

Experimental translocations reduced the total number of deer mice on the Cat Canyon murrelet monitoring plot during the nesting season compared to control areas. Trapping did not result in an immediate reduction in mouse abundance on the murrelet monitoring plot; rather, there was a delay of about 1 month before the number of mice caught began to decline from pre-removal levels, which underscores the extremely high densities of mice in the Cat Canyon area and island-wide in many years (Millus, 2006). Further, we were unable to keep mouse populations low throughout the entire

murrelet breeding season, which would have required a considerably higher trapping effort. Because mouse densities remained high (>120 ha⁻¹) off-colony on SBI throughout spring 2004 (Millus, 2006), areas surrounding the removal grid provided an ample source of immigrants. When resident mice from the colony were removed, individuals from neighboring areas were free to move onto the vacated area during periods when mice were not trapped. Nevertheless, our trapping efforts were sufficient to significantly reduce the numbers of resident mice.

Because fewer than 47 nests are initiated at the Cat Canyon monitoring plot each season (representing <5% of the estimated 1500 breeding pairs on the island), on average, only 65 eggs are laid at the Cat Canyon colony each year (range 42–90; Table 2). Eggs are likely incidental prey (*sensu* Vickery et al., 1992) for deer mice and are therefore only encountered opportunistically during searches for other prey. Indeed, stable carbon and nitrogen isotope analysis of mouse tissues suggested that murrelets do not comprise a major proportion of the diets of deer mice in murrelet colonies on SBI (Millus, 2006). The fact that murrelets may not be a major prey item for mice does not diminish the potential importance of egg predation by mice as a determinant of murrelet nest success, however, especially given the large numbers of mice on the island compared to the number of eggs laid and the movement abilities of mice.

The low rates of egg predation and high nest productivity we observed during our mouse control experiment support the contention that mice are important predators on murrelet eggs on SBI. The rate of egg predation (20.5%) was significantly lower, and nest productivity was significantly higher, during the mouse control period in 2004 than the average over the surrounding 12 years. Although our results suggest that reducing mouse abundance improved reproductive success, egg predation seems to have declined in Cat Canyon during the past 5–7 years (Fig. 4). Productivity has also tended to increase over this period (Table 2), though not as consistently because of inter-annual variation in the number of eggs that are abandoned, added or lost. This suggests that mouse control in 2004 may not have been the only factor affecting murrelet productivity.

Murray et al. (1983) suggested that rates of egg mortality may be influenced by a myriad of complex interactions among murrelets, deer mice, and barn owls, which prey upon adult murrelets when they come to SBI to nest. These interac-

tions may, in turn, be mediated by the effects of climate and marine productivity on the availability of food resources for mice and murrelets, respectively. Deer mouse populations fluctuate greatly between years because of inter-annual variation in rainfall and hence, abundance of food, especially seeds and insects (Drost and Fellers, 1991). Resident owls track deer mouse populations and their numbers tend to crash as mouse numbers decline. Risk of predation for adult murrelets, therefore, may be highest during periods of low mouse abundance, when owls are abundant and searching for alternate prey. Because the rocky, shrubby substrates typical of murrelet colonies are high-quality habitat for mice (Millus, 2006) and serve as refugia for remaining mouse populations on the island (Drost and Fellers, 1991), hunting activity of owls may be concentrated in colonies at times of low mouse abundance, which increases exposure of murrelets to owls. Also, predation on murrelet eggs may be greatest during periods when terrestrial productivity is extremely low, and mice are forced to search for alternate foods. This may be particularly critical in years when marine productivity is low because murrelets will be in poorer body condition and parents will be forced to leave eggs unattended for longer periods to forage, which will increase their vulnerability to predation (Murray et al., 1983; Roth et al., 2005). Alternatively, murrelet eggs may also be vulnerable in years of high owl predation, when adults are killed and eggs are abandoned.

There are no clear patterns in mouse population densities on SBI that could explain why nest predation rates might be declining. Habitat quality for mice in colonies may have deteriorated over time as a result of monitoring activity, but mice remain extremely abundant in colonies and island-wide (Millus, 2006). Consistent records of owl abundance were not available for SBI, but, because owl numbers track mouse numbers, it is unlikely that numbers of owls on SBI has decreased in recent years. A shift to cooler, more productive waters occurred in the Southern California Bight during the 1999–2002 La Niña (Schwing et al., 2002), and a cool regime continued into early 2005 (Goericke et al., 2005). As a result, mean spring macrozooplankton abundance was much higher ($\bar{X} = 159.11 \pm 68.29 \text{ ml } 1000 \text{ m}^{-3}$) between 1999 and 2004 than between 1993 and 1998 ($\bar{X} = 70.46 \pm 40.65 \text{ ml } 1000 \text{ m}^{-3}$). Higher macrozooplankton abundance from 1999 to 2004 may have meant that murrelets spent less time foraging at sea and more time attending eggs, which were therefore less vulnerable to predation. Changes in prey availability cannot completely account for reduction in nest predation, however. Egg predation was high (69%) in 2002, when mean spring macrozooplankton abundance was also relatively high ($\bar{X} = 140 \text{ ml } 1000 \text{ m}^{-3}$; macrozooplankton data from Scripps Institute of Oceanography, 1993–2004).

Given the high densities of mice in colonies relative to the numbers of eggs laid, some fraction (20–30%) of eggs may always be at risk of being eaten, even during poor mouse years. Nest predation therefore may be a major determinant of murrelet reproductive success only during periods when typical foods of mice are scarce. Schwemm and Martin (2005) found no correlation between egg predation and mouse abundance, but it is interesting that years when estimates of nest predation were unusually high (>50%; 1994, 1997, 2002; Fig. 4) were also years with low mouse densities elsewhere on SBI

(Schwemm and Martin, 2005) and, in 1994 and 2002, low winter rainfall (256 mm and 119 mm, respectively, from October–April; data from Airport, Santa Catalina Island). Mice were abundant island-wide in the summer of 2003 (Millus, 2006), but winter rainfall in 2004 was low (170 mm). We therefore would have predicted higher rates of egg predation in 2004 than in other years (2001, 2003 and 2005), when winter rainfall was much higher (414–790 mm), and the primary foods of mice would have been plentiful. If this was the case, our removal experiment may have actually reduced egg predation in a year when mice would have been expected to have been important egg predators.

In most years, approximately 20% of egg failures in Cat Canyon are due to factors other than predation; in 2004, 53% of egg failures were not attributed to mice. We speculate that, when present at high densities, deer mice may consume significant numbers of eggs that would not have hatched for other reasons. If so, our removal experiment may have revealed that rates of egg abandonment or death on SBI are higher than previously suspected, and, possibly, more similar to those on the San Benito Islands off Baja California, Mexico, where terrestrial predators are absent and abandonment accounts for 41–69% of egg failures of Xantus's Murrelets (Wolf et al., 2005). If eggs that were recorded as depredated were actually abandoned eggs that were subsequently scavenged by mice, then previous estimates of nest predation on SBI may have overstated the importance of mouse predation as the main cause of nest failure on SBI. Other factors, such as prey availability or adult mortality, may in fact be more important in affecting murrelet reproductive success, and should arguably be the focus on management efforts.

4.1. Management implications

The reduction of deer mice abundance in Xantus's Murrelet colonies on SBI may be a short-term strategy for reducing immediate threats of predation to eggs and chicks, especially when conducted on a local scale, and during years when risk of egg predation is expected to be high. Our removal experiment decreased egg predation by nearly 50% compared to historical estimates, the level of reduction that stabilized or resulted in a slight increase in population growth in the viability models constructed by Sydesman et al. (1998). However, the Cat Canyon monitoring plot represents only a small fraction (<12%) of the murrelet breeding population on SBI (Burkett et al., 2003), albeit one of only two areas that can be consistently and safely monitored. Intensive mouse control at one or a few colonies may improve local murrelet productivity, but it is not clear that it would substantially increase productivity of the breeding population on SBI. For mouse removal to be an effective tool for increasing murrelet nest success, it would need to be applied simultaneously to several colonies where the concentration of nesting murrelets is high. Removals would need to be implemented on a per-colony basis because island-wide eradication of endemic deer mice on SBI is not permitted under existing NEPA guidelines. Even if colonies were accessible, removal of mice from multiple areas would require intensive labor over a long period of time, which may be cost-prohibitive. Considering the labor required for this study (>4.5 person-h d^{-1} for 3 mo), maintaining

removals at several colonies would require many field personnel and substantial resources, in addition to those required to monitor murrelet nest success.

Although Sydeman et al. (1998) argued that reducing egg loss may be more effective and feasible than reducing adult mortality, control efforts aimed at predators of adult murrelets such as barn owls may offer an alternative or additional means of increasing murrelet numbers. Between 16 and 130 adult murrelets on SBI were observed killed each year by barn owls in monitored areas between 1982 and 1987 (Drost, 1989); barn owls were also believed to have contributed to the local extirpation of burrowing owls (*Athene cunicularia*) from SBI (Drost and McCluskey, 1992). Reduction of owl predation may be more cost-effective than mouse control because it can be applied over a much larger spatial scale, including areas where mice cannot be removed, and implemented over a shorter period of time. However, the effect of removing owls on the mouse population also needs to be considered. Removing owls from SBI may reduce mouse mortality, which may lead to increase predation on murrelet eggs. Additional studies of the ecology of barn owls on SBI, and their impacts on both mice and murrelets, and the relative importance of egg versus adult murrelet mortality, are necessary to determine whether such control efforts are feasible or would be effective in light of CINP's other conservation goals.

Lastly, we emphasize that, despite the attention directed at mice, threats to murrelets are not limited to land. Adult survival is often considered to be the most important life-history parameter for populations of long-lived seabirds such as Xantus's Murrelet, which typically have high adult survival and relatively low reproductive rates (Croxall and Rothery, 1991). Because murrelets spend most of their life at sea, survival is affected by availability of marine foods and mortality associated with the marine environment. Terrestrial threats may appear to be more manageable, but the reduction of mortality on land alone should not be expected to improve murrelet breeding population sizes if threats at sea are not simultaneously mitigated. Conservation of murrelets and the marine environment should not be overlooked or abandoned in favor of seemingly more tractable measures on land. Oil pollution and fisheries by-catch, for example, are known sources of mortality that remain under-studied (Carter et al., 2000). Moreover, management actions to benefit reproductive success of birds, such as those demonstrated in our study, are not always translated into long-term increases in the size of breeding populations (Côté and Sutherland, 1997). Because multiple, interacting factors influence long-term viability of Xantus's Murrelet populations, reducing mouse predation alone on SBI may not reverse the recent population decline. Concerted conservation actions directed at broad spatial scales, and that involve efforts both on land and at sea, may represent the best approach for maintaining stable murrelet populations on the California Channel Islands for the long term.

Acknowledgements

We thank H. Johnson for assistance in the field, M. Horn and D. Sandquist for their invaluable advice, and C. Schwemm

(CINP) for access to unpublished data and for field advice and support. We greatly appreciate the cooperation and logistical support provided by CINP. Funding was provided by Pittsburg Zoo Conservation Fund, California State University Special Fund for Research, and the Department of Biological Science at California State University, Fullerton. Comments from H. Carter and two anonymous reviewers greatly improved the manuscript.

REFERENCES

- Ashely, M., Wills, C., 1987. Analysis of mitochondrial DNA polymorphisms among Channel Island deer mice. *Evolution* 41, 854–863.
- Blight, L.K., Ryder, J.L., Bertram, D.F., 1999. Predation by Rhinoceros Auklet eggs by a native population of *Peromyscus*. *Condor* 101, 867–871.
- Bradley, J.E., Marzluff, J.M., 2003. Rodents as nest predators: influences on predatory behavior and consequences to nesting birds. *The Auk* 120, 1180–1187.
- Burkett, E.E., Rojek, N.A., Henry, A.E., Fluharty, M.J., Comrack, L., Kelly, P.R., Mahaney, A.C., Fien, K.M., 2003. Report to the California Fish and Game Commission: Status Review of Xantus's Murrelet (*Synthliboramphus hypoleucus*) in California. California Department of Fish and Game, Habitat Conservation Planning Branch Status Report 2003–01. 96pp. plus appendices.
- Carter, H.R., McChesney, G.J., Jaques, D.L., Strong, C.S., Parker, M.W., Takekawa, J.E., Jory, D.L., Whitworth, D.L., 1992. Breeding populations of seabirds in California, 1989–1991. Unpublished report, U.S. Fish and Wildlife Service, Northern Prairie Wildlife Research Center, Dixon, California.
- Carter, H.R., Whitworth, D.L., Takekawa, J.Y., Keeney, T.W., Kelly, P.R., 2000. At-sea threats to Xantus' Murrelets (*Synthliboramphus hypoleucus*) in the Southern California Bight. In: Browne, D.R., Mitchell, K.L., Chaney, H.W. (Eds.), *Proceedings of the Fifth California Islands Symposium*. U.S. Minerals Management Service, Camarillo, CA. 12pp.
- Carter, H.R., Sealy, S.G., Burkett, E.E., Piatt, J.F., 2005. Biology and conservation of Xantus's Murrelet: discovery, taxonomy and distribution. *Marine Ornithology* 33, 81–87.
- Côté, I.M., Sutherland, W.J., 1997. The effectiveness of removing predators to protect bird populations. *Conservation Biology* 11, 395–405.
- Croxall, J.P., Rothery, P., 1991. Population regulation of seabirds: implications of their demography for conservation. In: Perrins, C.M., Lebreton, J.D., Hiron, G.J.M. (Eds.), *Bird Population Studies*. Oxford University Press, Oxford, pp. 272–296.
- Drever, M.C., Blight, L.K., Hobson, K.A., Bertram, D.F., 2000. Predation on seabird eggs by Keen's mice (*Peromyscus keenii*): using stable isotopes to decipher the diet of a terrestrial omnivore on a remote offshore island. *Canadian Journal of Zoology* 78, 2010–2018.
- Drost, C.A., 1989. Predation and population cycles on a southern California island. M.S. Thesis, University of California, Davis, Davis, CA, USA.
- Drost, C.A., Fellers, G.M., 1991. Density cycles in an island population of deer mice, *Peromyscus maniculatus*. *Oikos* 60, 351–364.
- Drost, C.A., McCluskey, R.C., 1992. Extirpation of alternative prey during a small rodent crash. *Oecologia* 92, 301–304.
- Drost, C.A., Lewis, D.B., 1995. Xantus' Murrelet (*Synthliboramphus hypoleucus*). In: Poole, A., Gill, F. (Eds.), *The Birds of North America*. The Academy of Natural Sciences and The American

- Ornithologists' Union, Philadelphia and Washington, DC, 23pp.
- Efford, M., 2004. Density estimation in live-trapping studies. *Oikos* 106, 598–610.
- Evans, P.G.H., 1984. Status and conservation of seabirds in northwest Europe (excluding Norway and the USSR). In: Croxall, J.P., Evans, P.G.H., Schreiber, R.W. (Eds.), *Status and Conservation of the World's Seabirds*. ICBP Publication No. 2, Cambridge, U.K., pp. 293–320.
- Furness, R.W., Monaghan, P., 1987. *Seabird Ecology*. Blackie & Son Ltd., London.
- Gaston, A.J., 2004. *Seabirds: A Natural History*. A&C Black Publishers Ltd., London.
- Goericke, R., Venrick, E., Mantyla, A., Bograd, S.J., Schwing, F.B., Huyer, A., Smith, R.L., Wheeler, P.A., Hooff, R., Peterson, W.T., Chavez, F., Collins, C., Marinovic, B., Lo, N., Gaxiola-Castro, G., Durazo, R., Hyrenbach, K.D., Sydeman, W.J., 2005. The state of the California current 2004–2005: still cool? *CalCOFI Reports* 46, 32–71.
- Guillemette, M., Brousseau, P., 2001. Does culling predatory gulls enhance the productivity of breeding common terns? *Journal of Applied Ecology* 38, 1–8.
- Halvorson, W.R., Clark, R., Soiseth, C., 1992. Rare plants of Anacapa, Santa Barbara, and San Miguel in Channel Islands National Park. Technical Report. Cooperative National Park Studies Unit, University of California, Davis. 134pp.
- Hobson, K.A., Drever, M.C., Kaiser, G.W., 1999. Norway rats as predators of burrow-nesting seabirds: insights from stable isotope analysis. *Journal of Wildlife Management* 63, 14–25.
- Jones, H.P., Williamhenry III, R., Howald, G.R., Tershy, B.R., Croll, D.A., 2005. Predation of artificial Xantus's murrelet (*Synthliboramphus hypoleucus scrippsii*) nests before and after black rat (*Rattus rattus*) eradication. *Environmental Conservation* 32, 320–325.
- Karnovsky, N.J., Spear, L.B., Carter, H.R., Ainley, D.G., Amey, K.D., Ballance, L.T., Briggs, K.T., Ford, R.G., Hunt Jr., G.L., Keiper, C., Mason, J.W., Morgan, K.H., Pitman, R.L., Tynan, C.T., 2005. At-sea distribution, abundance and habitat affinities of Xantus's Murrelets. *Marine Ornithology* 33, 89–104.
- Keedwell, R.J., Maloney, R.F., Murray, D.P., 2002. Predator control for protecting kaki (*Himantopus novaezelandiae*) – lessons from 20 years of management. *Biological Conservation* 105, 369–374.
- Kirkpatrick, R.D., Rauzon, M.J., 1986. Foods of feral cats *Felis catus* on Jarvis and Howland Islands, central Pacific Ocean. *Biotropica* 18, 72–75.
- Martin, J.L., Thibault, J.C., Bretagnolle, V., 2000. Black rats, island characteristics and colonial nesting birds in the Mediterranean: consequences of an ancient introduction. *Conservation Biology* 14, 1452–1466.
- Martínez-Gómez, J.E., Jacobsen, J.K., 2004. The conservation status of Townsend's shearwater *Puffinus auricularis auricularis*. *Biological Conservation* 116, 35–47.
- Mayer, P.M., Ryan, M.R., 1991. Electric fences reduce mammalian predation on piping plover nests and chicks. *Wildlife Society Bulletin* 19, 59–62.
- Millus, S.A., 2006. Interactions between endemic deer mice and seabirds on Santa Barbara Island, California. M.S. Thesis, California State University, Fullerton, California, USA.
- Moorhouse, R., Greene, T., Dilks, P., Powlesland, R., Moran, L., Taylor, G., Jones, A., Knegtmans, J., Wills, D., Pryde, M., Fraser, I., August, A., August, C., 2003. Control of introduced mammalian predators improves kaka *Nestor meridionalis* breeding success: reversing the decline of a threatened New Zealand parrot. *Biological Conservation* 110, 33–44.
- Morris, R.D., Blokpoel, H., Tessier, G.D., 1992. Management efforts for the conservation of common tern (*Sterna hirundo*) colonies in the Great Lakes: two case histories. *Biological Conservation* 60, 7–14.
- Murray, K.G., Winnett-Murray, K., Eppley, Z.A., Hunt Jr., G.L., Schwartz, D.B., 1983. Breeding Biology of the Xantus' Murrelet. *Condor* 85, 12–21.
- Nordström, M., Hogmander, J., Laine, J., Nummelin, J., Laanetu, N., Korpimäki, E., 2003. Effects of feral mink removal on seabirds, waders, and passerines on small islands in the Baltic Sea. *Biological Conservation* 109, 359–368.
- Norman, F.I., 1971. Predation by the fox (*Vulpes vulpes* L.) on colonies of the short-tailed shearwater (*Puffinus tenuirostris* (Temminck)) in Victoria, Australia. *Journal of Applied Ecology* 8, 21–32.
- Otis, D.L., Burnham, K.P., White, G.C., Anderson, D.R., 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 62, 1–135.
- Pacific Seabird Group, 2002a. Petition to list Xantus' Murrelets (*Synthliboramphus hypoleucus*) as threatened. Letter and petition submitted to California Fish and Game Commission.
- Pacific Seabird Group, 2002b. Petition to list Xantus' Murrelets (*Synthliboramphus hypoleucus*) as Threatened. Letter and petition submitted to U.S. Fish and Wildlife Service.
- Philbrick, R.N., 1972. The plants of Santa Barbara Island, California. *Madroño* 21, 329–393.
- Roth, J.E., Sydeman, W.J., Martin, P., 2005. Xantus's Murrelet breeding relative to prey abundance and oceanographic conditions in the Southern California Bight. *Marine Ornithology* 33, 115–121.
- Schwemm, C.A., Martin, P.L., 2005. Response of nest success of Xantus's murrelets (*Synthliboramphus hypoleucus*) to native predator abundance, Santa Barbara Island, California. In Garcelon, D.K., Schwemm, C.A. (Eds.) *Proceedings of the Sixth California Island Symposium*. Ventura, California, pp. 373–384.
- Schwing, F.B., Bograd, S.J., Collins, C.A., Gaxiola-Castro, G., Garcia, J., Goericke, R., Gomez-Valdez, J., Huyer, A., Hyrenbach, K.D., Kosro, D.M., Lavaniegos, B.E., Lynn, R.J., Mantila, A.W., Ohman, M.D., Peterson, W.T., Smith, R.L., Sydeman, W.L., Venrick, E., Wheeler, P.A., 2002. The state of the California current, 2001–2002: will the California current system keep cool, or is El Niño looming? *CalCOFI Reports* 43, 31–68.
- Scripps Institute of Oceanography (SIO) Data Reports, 1993–2004. Macrozooplankton biomass data: April CalCOFI cruises. Scripps Institute of Oceanography, University of California.
- Seymour, A., Varnham, K., Roy, S., Harris, S., Bhageerutti, L., Church, S., Harris, A., Jennings, N.V., Jones, C., Khadun, A., Mauremootoo, J., Newman, T., Tatayah, V., Webbon, C., Wilson, G., 2005. Mechanisms underlying the failure of an attempt to eradicate the invasive Asian musk shrew *Suncus murinus* from an island nature reserve. *Biological Conservation* 125, 23–35.
- Stapp, P., 2002. Stable isotopes reveal evidence of predation by ship rats on seabirds on the Shiant Islands, Scotland. *Journal of Applied Ecology* 39, 831–840.
- Sydeman, W.J., Nur, N., Martin, P., 1998. Population viability analyses for endemic seabirds on the California marine ecosystem: the ashy storm-petrel (*Oceanodroma homochroa*) and Xantus's Murrelet (*Synthliboramphus hypoleucus*). Final Report to USGS Biological Resources Division, Species at Risk Program (formerly National Biological Service), Washington, DC.
- Vickery, P.D., Hunter Jr., M.L., Wells, J.V., 1992. Evidence of incidental nest predation and its effects on nests of threatened grassland birds. *Oikos* 63, 281–288.
- Whitworth, D.L., Carter, H.R., Young, R.J., Koepke, J.S., Gress, F., Fangman, S., 2005. Initial recovery of Xantus's Murrelets following rat eradication on Anacapa Island, California. *Marine Ornithology* 33, 131–137.
- Wolf, S., Phillips, C., Zepeda-Dominguez, J.A., Albores-Barajas, Y., Martin, P., 2005. Breeding biology of Xantus's Murrelet at the San Benito Islands, Baja California, Mexico. *Marine Ornithology* 33, 123–129.