RESPONSE OF NEST SUCCESS OF XANTUS'S MURRELETS (*SYNTHLIBORAMPHUS HYPOLEUCUS*) TO NATIVE PREDATOR ABUNDANCE, SANTA BARBARA ISLAND, CALIFORNIA

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Abstract—Xantus's murrelets (*Synthliboramphus hypoleucus*) and deer mice (*Peromyscus maniculatus elusus*) co-occur on Santa Barbara Island, California, throughout the murrelet breeding season. Deer mice are known egg predators of murrelets, and often reach extremely high population densities. Xantus's murrelets were recently listed by the State of California as a Threatened species, and protection from predation by mice on this island has been proposed as a potential mitigation action. Population monitoring data collected for both species between 1993 and 2002 were analyzed to determine whether annual changes in deer mouse densities were associated with changes in egg predation rates or productivity of Xantus's murrelets. We found no relationships between variation in mouse density and levels of egg predation, measures of hatching success, or productivity in murrelets. We also found mouse densities to be consistently higher in native habitat compared with non-native grasslands, suggesting that human-induced land-cover changes have not resulted in increased mouse densities on the island. We propose that annual variability in murrelet nest success on Santa Barbara Island is not related to changes in mouse population densities, and that predation impacts by mice have not increased over time. Nest predation by native mice should not be considered a cause of declines in murrelets across their range.

Keywords: Channel Islands, deer mice, ecological monitoring, nest predation, Xantus's murrelet

INTRODUCTION

Oceanic islands have long been recognized as critical habitat areas for nesting seabirds (Rodway 1991, Coulson 2002) due to the proximity of marine food resources and the general absence of mainland predators (Nelson 1980, Furness and Monaghan 1987). When non-native predators have been introduced to islands the resulting impacts to bird populations have often been catastrophic; in many cases breeding birds have been completely extirpated from an island in a relatively short period of time following the arrival of an exotic predator (Moors and Atkinson 1984, Dowding and Murphy 2001). However in a few examples seabirds and terrestrial predators have coevolved on islands, and in the absence of extrinsic disturbances each group has persisted over time in a stable predator-prey relationship (Moors and Atkinson 1984, Drever et al. 2000). Such a system is found on Santa Barbara Island, California (SBI), where the highest population of breeding Xantus's murrelets (*Synthliboramphus hypoleucus*; Murray et al. 1983, Drost and Lewis 1995, Pacific Seabird Group 2002, Burkett et al. 2003), coexists with a population of native deer mice (*Peromyscus maniculatus elusus*) that exists at densities as high as ever recorded for the species (Drost and Fellers 1991, Schwemm and Coonan 2001).

The worldwide population of Xantus's murrelets is in decline (Carter et al. 1992, Sydeman et al. 1998, Pacific Seabird Group 2002), and the species was recently listed as Threatened by the State of California. Predation by both native and non-native species has been identified as a threat to Xantus's murrelet productivity (Drost and Lewis 1995, McChesney and Tershy 1998), and the impact of predation by invasive black rats (*Rattus rattus*) on murrelets on Anacapa Island was one of the primary reasons rats were recently removed from that island (National Park Service 2002). The relationship between murrelet abundance and the population dynamics of native predators, however, has received less attention. Short-term direct impacts of predation by barn owls (*Tyto alba*) and deer mice on murrelets on SBI have been noted by several authors (Murray et al. 1983, Drost and Lewis 1995, Sydeman et al. 1998), but murrelet productivity has never been compared with the population dynamics of predators over longer periods. It is also unclear how nest predation rates affect long-term murrelet population stability, or whether human activities have indirectly altered the predator-prey balance between mice and murrelets. Several authors have suggested that conversion of island vegetation from mostly coastal shrub to predominantly exotic grasslands during the last century has resulted in greater population densities of mice (Salas 1990, D'Antonio et al. 1992, Halvorson et al. 1997, Sydeman et al. 1998), but this hypothesis has never been tested.

Although mice are assumed to be the cause of murrelet egg loss on SBI, very little is known about the actual mechanics of mouse consumption of eggs. Murrelet eggs are quite large (approximately 54 x 36 mm; Drost and Lewis 1995) and previous studies of *P. maniculatus* have found the species unable to consume eggs of this size (Bradley and Marzluff 2003). However there are no other explanations for broken and disappeared eggs. The only other non-marine vertebrate species on the island is the island night lizard, *Xantusia riversiana*, which is far too small to consume murrelet eggs (Fellers and Drost 1991). There is also no evidence that avian predators have ever taken murrelet eggs; the majority of murrelet nests on the island are located in small burrows and crevices, sites too small for potential predaceous birds such as western gulls (*Larus occidentalis*) to enter, and gulls have never been observed preying on eggs in vegetation-associated nests. Since there are no other alternatives, previous murrelet studies on the island have assumed that depredation by mice is responsible for all broken eggs and possibly for all eggs that disappear from nests (Murray et al. 1983, Drost and Lewis 1995, Sydeman et al. 1998, Burkett et al. 2003), and we initiated this study under those assumptions.

The natural co-existence of mice and murrelets on Santa Barbara Island begs closer observation for two reasons. First, the relationship represents an unusual example of a seabird species colonizing an island in the presence of a native terrestrial predator (Drever et al. 2000). Better defining the relationship between nesting murrelets and mouse population dynamics will therefore contribute to what is currently known about the population biology of murrelets. More immediately, understanding the degree to which egg predation limits murrelet productivity will facilitate the most effective allocation of resources toward murrelet conservation (Burkett et al. 2003). The direct effects of egg predation on murrelet nest success are examined in an associated paper (Schwemm et al. 2005), and in the present study we compare annual variability in mouse abundance on the island with murrelet productivity to identify key elements of this relationship.

STUDY AREA AND METHODS

Study Area

Santa Barbara Island lies centrally within the eight California Channel Islands, but is the farthest east and south of the five islands within Channel Islands National Park. The island is 2.6 km^2 in size, and ranges in elevation from sea level to 200 meters. Rainfall averages 46 cm per year, and temperatures during the spring average about 19ºC (Channel Islands National Park unpubl. weather data). Alien grasslands are the most abundant vegetation community on the island, and likely replaced historically abundant coastal scrub communities, particularly those dominated by giant coreopsis (*Coreopsis gigantea;* Philbrick 1972, Halvorson et al. 1988, Clark and Halvorson 1990, Junak et al. 1993).

Xantus's murrelets are monitored at the two sub-colonies (hereafter colonies) on the island most accessible to observers (Fig. 1). The Nature Trail (NT) colony is located adjacent to and below the housing complex on the east side of the island. The site is about 0.2 ha in area and includes 51 monitored nest sites on rocky cliffs. Native shrubs, including *Eriophyllum nevinii*, *Hemizonia* spp., and *Eriogonum giganteum* are interspersed with exotic grasses and provide most of the nesting habitat (Murray 1980, Murray et al. 1983, Lewis et al. 1988). The Cat Canyon (CC) site is on the south point of the island and includes 71 monitored nest sites. This colony is about 0.5 ha in size and is characterized by fewer shrubs and a greater abundance of native cactus (*Opuntia prolifera*), and exotic iceplant (*Mesembryanthemum crystallinum*). Birds here nest primarily in rock crevices rather than under vegetation.

Sampling Methods

Data describing nesting phenology, egg fate and site productivity for Xantus's murrelets have been collected annually since 1983. For this report we utilized data collected between 1993–2002 (Martin and Sydeman 1998, Roth et al. 1998, Roth et al. 1999, Wolf et al. 2000, NPS unpubl. data). Marked nest sites are checked every five days beginning March 5th until a 15-day period has elapsed without indication of additional nesting activity. Active sites are monitored until eggs hatch, are depredated or disappear. Egg fates are identified as broken, hatched, disappeared, addled (dead), abandoned, broken by humans or fate unknown. (Eggs are considered abandoned if left unattended for three or more surveys.) Experienced observers can distinguish between hatched and broken eggs; hatched eggs have a thick, papery, vascularized membrane and are broken around the fat end of the egg, while broken eggs have a shiny, adherent membrane and are often broken longitudinally. Other than damage by humans and predation, no additional processes have been identified that would result in broken eggs. Consequently within this report there is no distinction made between values for broken and depredated eggs.

Many of the eggs that disappear are laid in rocky crevices, and there are few explanations for their subsequent absence other than removal by mice. However because the fate of these eggs is not certain, for this analysis we classified predation as both measured (number of eggs broken) and assumed (number of eggs disappeared plus number of eggs broken). For the analyses we included both measured and assumed predation measurements. However there were no differences in the results between the two measures so our discussion addresses the results using assumed predation values only. Hatching success for each site was defined as the number of eggs hatched per number of eggs laid. Annual productivity for each site was measured both by the number of eggs hatched per nest sites occupied, and by the number of eggs hatched per nesting attempt. (Second and third nesting attempts generally occur only when initial clutches are completely lost.) Because previous studies and monitoring data have demonstrated differences in predation and productivity between the two sub-colonies, we analyzed the data from each site separately as well as combined.

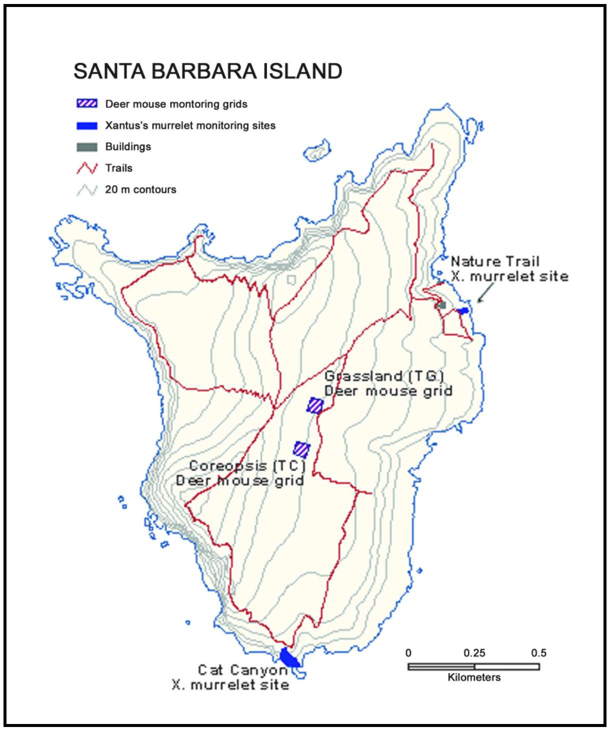

Figure 1. Location of Xantus's murrelet and deer mouse monitoring sites on Santa Barbara Island.

Deer mouse populations are sampled semi-annually in the spring and fall at two sites near the center of the island. These sites were selected to observe mouse population changes in the vegetation types that are most common on the island (Fellers et al. 1988). The TC grid is situated in an area dominated by *Coreopsis gigantea* (hereafter *Coreopsis*) shrubs. These stands typically have a thick canopy at the level of the leaves and flowers, about 1.0 – 1.5 meters high, but provide a relatively open understory where low-growing grasses and perennials are common. The TG grid is located in homogenous habitat dominated by wild oats (*Avena* spp.), brome grasses (*Bromus* spp.), and *Hordeum murinum*, and is similar in structure and composition to exotic annual grasslands on the other California Channel Islands.

Deer mouse density estimates were calculated from trapping data collected during the spring from 1993–2002 (Schwemm 1995, Schwemm 1996, Austin 1996, Austin 1998, Schwemm and Coonan

2001, NPS unpubl. data). Data were not collected in 1994 due to Hanta virus concerns and subsequent testing that year. Methodologies are described in the monitoring protocol (Fellers et al. 1988), and consist of semi-annual mark-recapture sampling for population abundance and demographics. Live traps are spaced 7 m apart in a 10- x 10-m grid and baited with dry oats for a minimum of three nights.

For this analysis we utilized density estimates calculated using the software program CAPTURE (White et al. 1982) with some interpretation. Evaluation of CAPTURE results are sometimes problematic; when animal populations are relatively high and recapture rates sufficient, CAPTURE provides a good estimate of real populations (Otis et al. 1978, Thompson et al. 1998). When few individuals are caught or when recapture rates are low, however, population estimates calculated from mark-recapture data are less reliable (White et al. 1982). Using the direct count of individuals as an index of population size is an alternative, although such a measure generally underestimates population size and consequently may not reflect real temporal variability (Slade and Blair 2000, McKelvey and Pearson 2001).

For all trapping periods when the number of individuals captured was greater than five we calculated population estimates using the heterogeneity model in CAPTURE with the Jackknife estimator (model M(h)). To estimate density, population estimates were divided by the effective trap area, calculated by adding the mean maximum distance moved (MMDM) as a strip width on all sides of the grid (Parmenter et al. 2003). Because it was important to include periods of low mouse densities within the analysis, for three cases when capture rates were very low (less than five individuals in 300 trap nights), we assigned those sessions a density value of 10/ha using the above method and a strip width as calculated by CAPTURE for the TC grid in March 1995.

Statistical Methods

Statistical analysis of all variables was conducted using SYSTAT v.10 (SPSS Inc. 2000). Linear regression was used to examine relationships between mouse densities and numbers of eggs laid, eggs depredated, hatching success and productivity. Paired *t*-tests were used to examine differences in predation and nesting variables between the sites. Arcsin transformations were performed on data describing percentage of eggs depredated and percentage of eggs hatched (Dytham 1999). An alpha value of 0.05 was used to determine significance of all statistical tests.

RESULTS

Nesting parameters for murrelets between 1993 and 2002 are provided in Table 1. Combined (both sites) average annual productivity per nest attempt ranged from 0.29 – 1.5, and hatching success from 0.19 – 0.86. Annual assumed predation at both sites, including broken and disappeared eggs, ranged from 0.0–68.9% of all eggs laid. Density estimates for mice for all sampling periods ranged from 10–443/ha (Table 2). In all years more individual mice were caught on the *Coreopsis* (TC) grid than on the grassland (TG) grid when both were sampled, however in two years density estimates were higher on the grassland grid.

We found no significant relationships between annual spring densities of mice and rates of predation, hatching success, or productivity of murrelets at either site from 1993–2002 (Table 3). Specifically, there were no correlations between mouse densities on either grid and the percentage of eggs depredated, actual number of eggs broken, or hatching success at either site or at sites combined. We also examined the data for indications of density-dependent predation behavior by mice. We found a significant relationship between the number of eggs laid and the number of eggs depredated at the NT ($r^2 = 0.715$, $F = 20.063$, $P = 0.002$) but not at the CC site ($r^2 = 0.155$, $F = 1.464$, $P = 0.261$). There were significantly more eggs laid at the CC site in all years ($t = 7.563$, $P = 0.000$, $df = 9$), however there was no difference in predation rates between sites as measured by percentage of eggs depredated ($t = 1.055$, $P = 0.319$, $df = 9$).

DISCUSSION

Our objective was to better understand whether changes in deer mouse abundance have direct impacts on murrelet nest success on SBI, and we approached this question from two perspectives.

Table 1. Results of Xantus’s murrelet monitoring at Cat Canyon (CC) and Nature Trail (NT) sites.

	YEAR																			
	1993		1994		1995		1996		1997		1998		1999		2000		2001		2002	
Parameter	CC	NT	CC	NT	CC	NT	CC	NT	CC	NT	CC	NT	CC	NT	CC	NT	CC	NT	CC	NT
Nests Occupied	41	24	38	18	30	15	33	24	36	18	36	19	45	12	33	8	35	8	31	8
Nest Attempts	42	24	42	18	30	16	34	26	48	28	47	22	53	14	35	8	38	8	44	8
Eggs laid	58	33	58	27	42	24	54	36	73	43	79	35	90	24	58	14	65	15	61	11
Eggs Hatched	34	20	27	10	23	9	32	13	22	8	39	16	46	8	39	12	45	12	18	3
Hatch success	0.59	0.61	0.47	0.37	0.55	0.38	0.59	0.36	0.30	0.19	0.49	0.46	0.51	0.33	0.67	0.86	0.69	0.80	0.29	0.27
Productivity per nest	0.83	0.83	0.71	0.56	0.77	0.6	0.97	0.54	0.61	0.44	1.08	0.84	1.02	0.67	1.18	1.5	1.29	1.5	0.58	0.38
Productivity per attempt	0.81	0.83	0.64	0.56	0.77	0.56	0.94	0.50	0.46	0.29	0.83	0.73	0.87	0.57	1.11	1.5	1.18	1.5	0.41	0.38
Measured predation (#eggs)	17	4	27	9	14	1	18	11	42	19	28	7	26	3	15	0	12	3	38	0
Assumed Predation (# eggs)	20	6	29	17	16	7	20	21	43	27	29	10	27	7	17	1	12	3	42	0
% Predation – Measured	29.3	12.1	46.6	33.3	33.3	4.2	33.3	30.6	57.5	44.2	35.4	20.0	28.9	12.5	25.9	0	18.5	20.0	62.3	0
% Predation – Assumed	34.5	18.2	50.0	63.0	38.1	29.2	37.0	58.3	59.0	62.8	36.7	28.6	30.0	29.2	29.3	7.1	18.5	20.0	68.9	0

Table 2. Dates and results of spring deer mouse monitoring at the Coreopsis (TC) and grassland (TG) sites.

Year	Dates of sampling		Total individuals		Population estimate with model M (h)		Effective trap area (m^2)		Density estimate (mice/ha)	
	TC	TG	TC	TG	TC	TG	TC	TG	TC	TG
1993	3–5 Mar.	3–5 Mar.	22	6	23	6	6,800	13,600	39	4.4
1995	1–3 Mar.	-	3	--	*	--	5,239	--	* 10[1]	--
1996	27–29 Mar.	27–29 Mar.	131	100	190	156	5,589	5,631	340	278
1997	19–21 Mar.	19–21 Mar.	19	14	28	20	6,777	7,878	41	25
1998	9–11 Apr.	9–11 Apr.	50	48	85	73	6,662	4,478	128	163
1999	5–7 Mar.	27–29 Mar.	2	1	*	*	*	*	* 10[1]	* 10[1]
2000	21–23 Apr.	-	43	--	48	--	6,892	--	70	--
2001	14–16 Mar.	13–15 Apr.	141	91	216	137	4,880	5,219	443	263
2002	16–18 Apr.	16–18 Apr.	44	40	56	75	7,389	6,571	76	114

-- no sampling conducted.

* capture rates too low for CAPTURE analysis.

[1] To include instances of very low densities in the analysis, a raw estimate of five individuals was divided by the calculated trap area for the TC grid, Mar. 1995 for each of these sessions.

First, we analyzed measurements of mouse population dynamics in exotic and native habitats to evaluate whether human-caused habitat conversion might have altered average mouse abundance on the island over the last century. We assumed that consistently higher numbers of animals in either the grasslands or the *Coreopsis* stands would indicate habitat preference by mice between the sites (Morin 1999). We found mouse numbers consistently higher in the *Coreopsis* habitat, suggesting that numbers of mice on the island have not increased over time due to conversion of native shrublands to alien annual grasslands. Second, we compared annual changes in mouse densities with same-year murrelet nest success; an inverse relationship between these two variables would suggest a direct impact of increased mouse abundance on egg survival (Schmidt and Ostfeld 2003). Our data show that mouse population dynamics appear to have very little if anything to do with murrelet nest success. For example, between 1993 and 2002 average

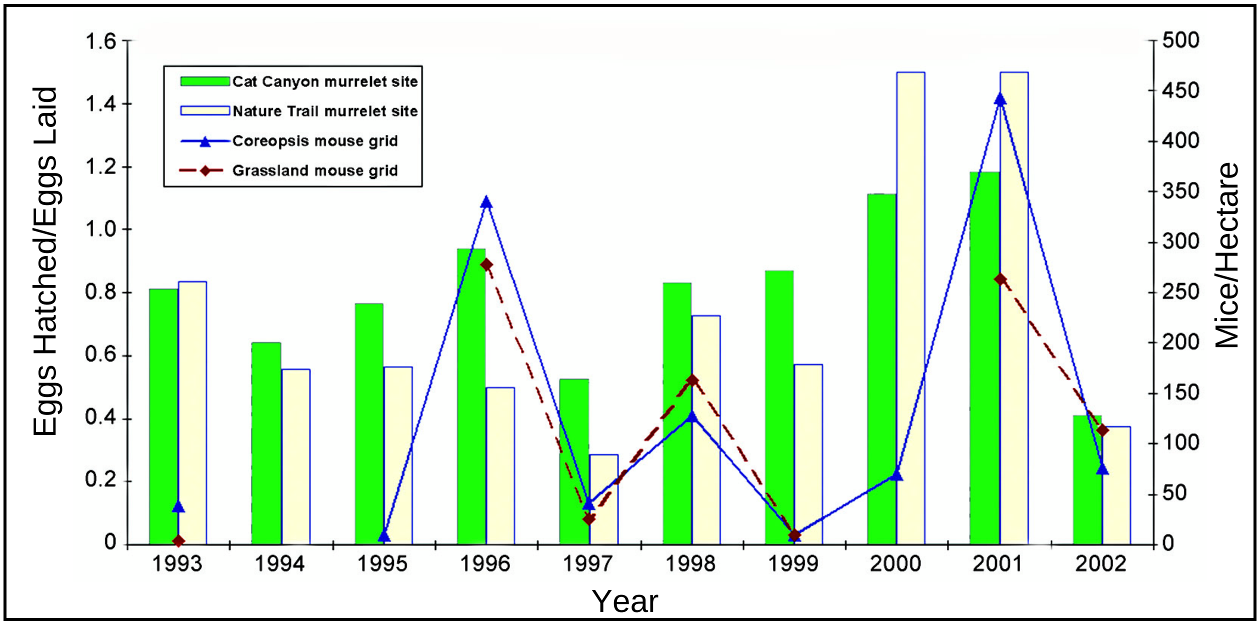

Figure 2. Mouse densities and average productivity per nest, Santa Barbara Island, 1993–2002.

Table 3. Relationship of mouse densities at the Coreopsis (TC) and grassland (TG) sites to murrelet reproductive success.

	Spring Mouse Densities					
	Coreopsis (TC)			Grassland (TG)		
Parameter	r^2	F	P	r^2	F	P
Cat Canyon						
% Eggs broken	0.143	1.168	0.316	0.102	0.567	0.485
% Assumed predation	0.173	1.465	0.265	0.102	0.568	0.485
Hatching success	0.234	2.143	0.187	0.249	1.660	0.254
Productivity per attempt	0.050	0.370	0.562	0.037	0.191	0.680
Nature Trail						
% Eggs broken	0.096	0.741	0.418	0.013	0.066	0.808
% Assumed predation	0.025	0.178	0.686	0.009	0.043	0.844
Hatching success	0.187	1.609	0.245	0.164	0.979	0.368
Productivity per attempt	0.159	1.319	0.288	0.195	1.211	0.321
Combined						
% Eggs broken	0.048	0.350	0.573	0.055	0.290	0.614
% Assumed predation	0.060	0.446	0.526	0.031	0.162	0.704
Hatching success	0.295	2.936	0.130	0.184	1.124	0.338
Productivity per attempt	0.119	0.948	0.363	0.126	0.724	0.434

productivity per nest at the CC site was greater than 1.0 when mouse densities were 280/ha as well as when they were 10/ha (Fig. 2). These results suggest that ecological factors other than mouse population dynamics determine murrelet nest success.

Habitat Use

Mouse densities in the native *Coreopsis* habitat were consistently higher than those in the non-native grassland. While there are non-native plant species present on the C*oreopsis* grid, the habitat is much more similar to that which likely dominated the island historically (Hochberg et al. 1979). Collins et al. (1979) also found mouse densities twice as high in *Coreopsis* habitat on SBI when compared to areas dominated by non-native iceplant (*Mesembryanthemum crystallinum*), and Drost and Fellers (1991) found mouse densities higher in *Coreopsis* and native *Sueda* habitats when compared to grassland areas. Because conditions on the island are so suitable for mice (mild weather, abundant food resources, absence of ground predators; King 1968), and because mice apparently prefer native habitats over exotic plant assemblages, we suggest that the mouse population always existed in very high numbers on SBI, and in fact may have been more abundant when shrubland habitat dominated the island than they are today.

This hypothesis is in contrast to one put forth by several previous studies suggesting that mouse densities and resulting levels of egg predation on the island are anthropogenically inflated by additional food resources provided by introduced plants (Murray et al. 1983, Pacific Seabird Group 2002). There is no evidence that mice prefer the food items available in grasslands, and we suggest that native shrublands provide both greater food resources and better protective cover than do grasslands or the more sparse habitats associated with murrelet colonies. Deer mice are characterized as generalist feeders throughout their range (Baker 1968) and both Collins et al. (1979) and Murray (1980) found that mice on SBI consumed a variety of foods, with a diet that differed spatially and between seasons but never included one food type exclusively. While exotic grasslands still dominate the SBI landscape (Junak et al. 1993), vegetation recovery in the last several decades has resulted in a slow but measurable increase in native shrub cover (Halvorson et al. 1997, Johnson 1998). These changes may be increasing habitat that provides greater foraging and protection opportunities for mice than do murrelet colonies (Morrison and Hall 1998, Jacob and Brown 2000).

Foraging Behavior

Changes in nest density within the colonies may also be indirectly affecting nest success. Island-wide nest occupancy by murrelets has declined over the last 20 years, apparently due to lower numbers of nesting adults (Burkett et al. 2003). Concurrently, predation rates at nests that are occupied also appear to be declining (Schwemm et al. 2005). Eggs are not a required element in mouse diets (Collins et al. 1979), and in fact several studies have provided examples of *Peromyscus* populations that select other foods even when eggs are available. Drever et al. (2000) found that during the seabird nesting season egg material made up at most 60% of the relative prey types in mouse diets on Triangle Island, B.C. Vickery et al. (1994) and Lewis et al. (2001) found that high protein content, as found in eggs, did not dictate food preference, and that deer mice often selected energy-rich foods, such as seeds, over protein-rich ones when offered the two simultaneously. Finally, several studies on rodents and songbird eggs have shown that egg predation can occur incidentally as mice forage for other foods (Vickery 1992, Schmidt et al. 2001). If a similar process is operating in the murrelet colonies on SBI, this kind of incidental predation would be expected to decrease as nest densities decline.

Breaking open eggs of this size is likely a great deal of work for mice (Bradley and Marzuff 2003), and this expenditure of energy certainly has some impact on mouse foraging strategies (Phelan and Baker 1992). Optimal foraging theory predicts that lowered prey densities, and in this case a prey type that requires a significant investment of time to procure (Bradley and Marzluff 2003), will cause mice to forage where food is more plentiful and protection from predators more likely (Phelan and Baker 1992, Mysterud and Ims 1998, Schmidt and Whelan 1999). Murrelet colonies may at this point be providing less food in the form of eggs than they did previously, causing mice to forage either in other areas or in these areas less often, with a resulting decline in egg predation (Schwemm et al. 2005).

The absence of a connection between higher mouse densities and increased rates of egg loss suggest the presence of other factors that limit hatching success. Nest abandonment is common in Xantus's murrelets (Drost and Lewis 1995, C. Phillips pers. comm.), accounting for a high proportion of nest failure in some years. For example at the NT site in 2002, 73% of the eggs laid were abandoned (8/11). Egg abandonment may be due to predation on adult birds by barn owls after eggs are laid (Drost and Lewis 1995), and owl numbers on the island in the spring of that year were extremely high (authors pers. obs.). Losses of adult murrelets to owls may also have been responsible for the lowest number of eggs laid or hatched at that site since 1993 (Table 1). The importance of owls within the system has frequently been discussed (Murray et al. 1983, Fellers and Drost 1991, Drost and Fellers 1991), and we suggest that future studies be designed specifically to address the relationship between owl population variability and murrelet nesting success.

Because seabirds are dependent on both marine and terrestrial resources, recovery of rare seabird populations is extremely challenging and requires an understanding of the ecology of birds within both systems. Determining the causes of the decline in Xantus's murrelets will be an important step toward murrelet recovery (Burkett et al. 2003), and will of necessity include significant focus on the important breeding colonies on Santa Barbara Island. Our results strongly suggest that neither short- nor long-term mouse population variability is responsible for reduced productivity of murrelets on the island and should not be considered a cause of the decline in murrelet abundance. Some level of nest protection may be required in the short-term to facilitate greater nest success, however we hope that such efforts do not divert important resources away from finding long-term solutions to murrelet recovery.

ACKNOWLEDGMENTS

Many people assisted with field work over the years, and we particularly thank G. Austin, H. David, S. Coppelli, and K. Rutz for work with mice, and C. Arnett, C. Baduini, G. Ballard, J. Boyce, M. DesLauriers, J. Feldman, T. Flaherty, B. Fulsom, D. Hardesty, P. Hartman, G. Hoffman, K. McCurdy, S. Meyers, R. Nelson, D. Nothhelfer, C.

Pickens, M. Shultz, L. Spadoni, S. Stapleton, S. Sturges, T. Winter, S. Thomé, S. Vaneaux, and G. Yanega for assistance with murrelets. Point Reyes Bird Observatory, especially B. Sydeman, J. Roth, and S. Wolf collected murrelet data as part of the monitoring program for many years. E. Creel and R. Young stepped in many times to assist the park with murrelet monitoring. C. Phillips provided information on murrelet nesting success in Baja. H. Carter and D. Whitworth also provided essential assistance while generously sharing expertise. C. Drost was an unending source of information regarding everything that lives on Santa Barbara Island. G. Hunt continuously supported the seabird monitoring program and provided a critical link to the early years of murrelet study on the island. T. Coonan assisted with statistical analysis, and P. Stapp, T. Coonan and especially M. Glassow provided insightful comments and helpful criticisms on earlier versions of the manuscript.

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