

NEST OCCUPANCY AND HATCHING SUCCESS OF XANTUS'S MURRELETS (*SYNTHLIBORAMPHUS HYPOLEUCUS*) BREEDING ON SANTA BARBARA ISLAND, CALIFORNIA DURING A TWENTY-YEAR PERIOD

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Abstract—Xantus' murrelets (*Synthliboramphus hypoleucus*) are small seabirds that nest on several of the California Islands. The worldwide population of Xantus's murrelets has declined, and the species was recently listed by the State of California as Threatened. Predation at breeding colonies was identified within the listing decision as a significant obstacle to murrelet recovery, however very little is known about how predation processes affect murrelet abundance. We investigated impacts of nest predation on Xantus's murrelets by native deer mice (*Peromyscus maniculatus*), by compiling nest occupancy and hatching success data obtained from annual monitoring of the primary breeding sub-colony on Santa Barbara Island, California, from 1983–2002. Mean nest occupancy rates declined over the 20-year period, whereas the mean number of eggs hatching in a nest when it was occupied increased. Consequently, the total number of eggs hatching from the sub-colony for the past twenty years has remained unchanged. Individual nest occupancy rates for the period varied among nests, with 17 nests occupied 16 or more years and the same number occupied fewer than six years. To investigate potential density-dependent effects on nest predation rates, we also analyzed GPS location information along with nest success data for each site. Nest success was not correlated to nest density among years. Likewise we detected no effect of nearest-neighbor distance on nest success, indicating that nearness to conspecifics did not influence the likelihood that a nest would produce a chick. Identification of long-term trends in nest occupancy and hatching success may assist in predicting future conditions and promote the success of recovery efforts aimed at protecting critical habitat areas for murrelets.

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

INTRODUCTION

Successful management of rare and endangered species requires a clear understanding of the autecology of populations at risk, as well as identification of the causes of population declines (Primack 1998). Occasionally these factors are evident, but more often there are multiple contributing factors or the primary causes are elusive. In the case of seabirds, identifying critical population regulating mechanisms may be particularly challenging because of seabird dependence on both marine and terrestrial resources (Kress 1998).

Nest predation is common throughout avian populations (Burger and Gochfeld 1994), and has been discussed extensively in many studies of seabird ecology (Buckley and Buckley 1980, Moors and Atkinson 1984, Burger and Gochfeld 1994). Most empirical studies of nest predation on seabirds have investigated impacts from non-native predators, a condition to which birds are typically unadapted and that threatens seabird populations worldwide (Moors and Atkinson 1984, Kress 1998). Fewer studies have examined systems where seabirds and native nest predators coexist, possibly because the condition appears to be

uncommon (Buckley and Buckley 1980, Drever et al. 2000). Blight et al. (1999) found that native Keen's mice (*Peromyscus keeni*) preyed heavily on rhinoceros auklet eggs (*Cerorhinca monocerata*). Drever et al. (2000) also investigated *P. keeni* predation on eggs of both rhinoceros and Cassins' auklets (*Ptychoramphus aleuticus*), and concluded that egg predation was a common occurrence within the mouse population. In laboratory experiments, Bradley and Marzluff (2003) found that two species of *Peromyscus* (*P. maniculatus* and *P. keeni*) were unable to consume marbled murrelet eggs (*Brachyramphus marmoratus*) due to their large size, but did exhibit aggressive behavior toward chicks. Murray et al. (1983) described predation of Xantus's murrelet eggs (*Synthliboramphus hypoleucus*) by *P. maniculatus elusus*, the two species of interest in this paper, and reported a 40–50% depredation rate in 1977 and 1978. However the long-term impacts of egg predation by native predators on seabird populations are unknown.

Xantus's murrelets are small seabirds that nest on islands off the coast of Southern California and Baja, Mexico, and the species was recently listed by the State of California as Threatened. Significant population declines for murrelets have been documented beginning in the mid-1970s (Carter et al. 1992, Sydeman et al. 1998, Burkett et al. 2003), however the causes for this decline are not understood. Impacts to birds at sea include oil pollution, entanglement in fishing gear, and reduced food resources (Carter et al. 2000, Sydeman et al. 2001), while on-land threats stem mostly from predation on adults and eggs as well as the loss of nesting habitat (Drost and Lewis 1995, Pacific Seabird Group 2002, Burkett et al. 2003). Of these known threats, the impacts of nest predation have received the most attention from many observers. Both the listing petition by the Pacific Seabird Group (2002) and the resulting Status Review (Burkett et al. 2003) specifically discuss the impacts of native deer mouse (*P. maniculatus elusus*) predation on murrelet eggs on Santa Barbara Island, where the primary nesting colony supports approximately 60% of the worldwide breeding population of murrelets (Murray et al. 1983, Drost and Lewis 1995, Burkett et al. 2003). Both documents strongly suggest that egg predation by mice significantly affects nest

success and is a major threat to murrelet population recovery (Pacific Seabird Group 2002, Burkett et al. 2003).

Our goal was to better define the role of nest predation by native predators within the larger population decline of Xantus's murrelets, and our objectives were threefold. First, we summarized the nest occupancy and success data from the Cat Canyon breeding sub-colony (hereafter 'colony') on Santa Barbara Island, and examined temporal trends in nest occupancy rates, hatching success, and number of eggs hatching from 1983–2002. Sydeman et al. (2001) evaluated nest success for the period 1985–1997, and annual reports from monitoring (for example Wolf et al. 2000), have presented nest success data for individual years, however the present paper presents the first cumulative summary of nest success information for the 20-year span of Xantus's murrelet monitoring. Second, we compared the monitoring data with GPS locations collected for each nest to determine if there were differences in nest success based on elevation or distance to neighboring nests. An observed influence of vertical position on nest success might suggest variable habitat use by mice (Schmidt and Ostfeld 2003b), for example in the higher areas of the colony where vegetation is more abundant and where possible impacts from greater mouse densities might be observed. Comparison of nearest-neighbor distance and overall nest density with nest success could provide indications of anti-predator benefits that result from increased nest densities, a strategy documented in many colonial nesting bird species (Goetmark and Andersson 1984, Massoni and Reboreda 2001), as well as information about the foraging behavior of *P. maniculatus*. Finally, we determined whether there were differences in cumulative hatching success between individual nests over the 20-year period. Such variation might indicate successful nest characteristics, factors that could be incorporated into habitat enhancement programs.

STUDY AREA AND METHODS

Santa Barbara Island (hereafter SBI) is centrally located within the eight California Channel Islands, and is the farthest island east and

south of the five islands within Channel Islands National Park. The island is 2.6 km² in size, and ranges in elevation from sea level to 200 m. Rainfall averages 46 cm per year, and temperatures during the spring average about 19°C (Channel Islands National Park unpubl. data). Exotic grasslands are the most common vegetation community on the island, and likely replaced historic coastal shrub communities, particularly those dominated by giant coreopsis (*Coreopsis gigantea*; Philbrick 1972, Halvorson et al. 1988, Clark and Halvorson 1990, Junak et al. 1993). The Xantus's murrelet monitoring site at Cat Canyon consists of approximately 0.5 hectares of mostly steep, rocky cliff faces on the south point of the island. The ground cover is characterized by sparse vegetation consisting of native cactus (*Opuntia prolifera*), and exotic iceplant (*Mesembrythemum crystallinum*), and murrelets nest primarily in rock crevices (Murray et al. 1983).

Ecological monitoring of nesting activity and success for Xantus's murrelets on Santa Barbara Island was conducted each spring from 1983–2002 by the National Park Service and cooperators. Prior to 1993 sites at Cat Canyon were checked approximately once per week and at least once every two weeks. Since 1993 sites have been checked every five days beginning on March 5. A small flashlight and/or mirror is used to survey the interior of crevice sites. If no birds are observed and the crevice is difficult to see into, the crevice is searched by hand to find any eggs that might be hidden from view. If a bird is observed, its presence is simply noted. If only an egg(s) is found, it is removed from the site, measured, and marked with a permanent felt-tip pen. Egg length and width are measured using Vernier calipers and the egg is replaced in the site in the same spot and same orientation in which it was found. Egg shells and shell fragments are collected to determine egg fate and to determine whether open eggs were depredated or have hatched. Depredated eggs are broken lengthwise and have shiny, adherent membranes. Hatched eggs are either broken in half with dry, papery membranes that have separated from the shell or they have no membranes at all. It may be determined that an egg has hatched if no egg shells or fragments are found but the egg was incubated for the appropriate amount of time. All sites are checked three times (15 days) past the date

of the last nest initiation. Active nests are followed until eggs are hatched or the site fails. A final check of all sites is performed after the last active nest has finished, ensuring that no late nesting or re-initiation was missed.

We analyzed yearly trends in nest occupancy and hatching success using Pearson product-moment correlation analysis. Specifically, we tested the strength of association between year (1983–2002) and annual nest occupancy rate at the colony, mean annual number of eggs hatching when nests were occupied, and the total annual number of hatched eggs in the Cat Canyon colony on Santa Barbara Island. For analyses on specific nest sites, we log-transformed the nest elevation data and arcsine-square-root-transformed nest occupancy rates to improve normality. We used correlation analysis to test the strength of association between nest occupancy rate (1983–2002) and the mean number of eggs hatching when the nest was occupied. We also used correlation analysis to test the strength of association between nest elevation (m) and nest occupancy rate, mean number of eggs hatching when the nest was occupied, and the total number of eggs hatching at that nest site during the 20-year period.

For the nearest-neighbor analysis, nest locations were recorded using a Trimble ProXR (Sunnyvale, California) differential global positioning system (GPS) and exported to ArcView® (Environmental Systems Research Institute – Redlands, CA) shape-files. Using ArcView we performed two types of nearest neighbor analyses: (1) all years pooled (1983–2002) and (2) for each year separately. For the first analyses, we used correlation analysis to test the strength of association between nearest neighbor distance (log-transformed) for each of the 64 nest sites and mean nest occupancy rates, mean number of eggs hatching when nests were occupied, and the total number of eggs hatching at each nest site (log-transformed) during the 20-year period. For the within year analyses, we used only those nest sites that were occupied that year to calculate nearest neighbor distances. Within years, nearest-neighbor effects were tested using logistic regression, where the nest's fate (successfully hatched ≥ 1 egg or unsuccessful) was the dependent variable and the distance to the nearest neighboring nest was the predictor variable. All means are reported ± 1 SD unless otherwise noted.

RESULTS

Trends in Nesting Ecology

The annual nest occupancy rate at the Cat Canyon breeding colony on SBI declined during 1983–2002 (Pearson correlation: $r = -0.52$, $n = 20$ years, $P = 0.02$), ranging from 0.70 in 1991 to 0.28 during the 2002 breeding season (Fig. 1). However, the mean annual number of eggs hatching when a nest was occupied increased during the same time period (Pearson correlation: $r = 0.40$, $n = 20$ years, $P = 0.08$; Fig. 2). These opposing trends have resulted in no relationship between year and the total number of eggs hatching from the Cat Canyon colony (Pearson correlation: $r = 0.01$, $n = 20$ years, $P = 0.96$). On average, 26.6 ± 9.6 eggs have hatched from the 64 nests in the Cat Canyon colony each year (Fig. 3).

Cumulative nest occupancy rate during the 20 year period varied considerably among nest sites and averaged 0.54 ± 0.27 . Of the 64 nests monitored, two nests were occupied every year and three nests were occupied only once (Fig. 4). Similarly, the number of eggs hatching when a nest was occupied varied among nest sites (Fig. 5) and averaged 0.69 ± 0.34 ; 16 nests consistently produced ≥ 1 hatched egg on average and four nests, though occupied in some years, never produced a hatched egg. In total, 13 nests produced 15 hatched eggs during the 20-year period (Fig. 6). Mean nest occupancy rate during the 20-year

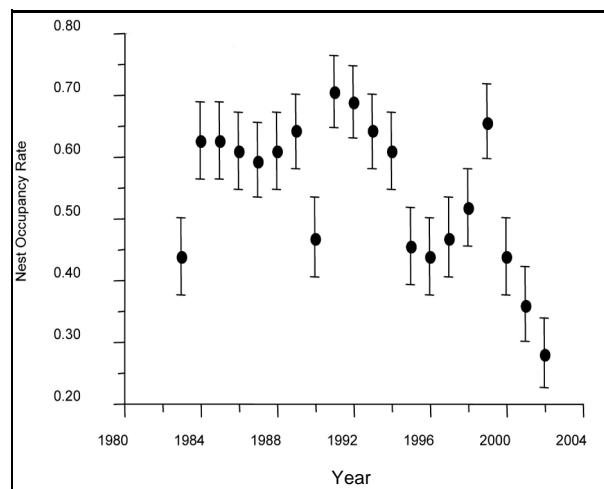


Figure 1. Cumulative Xantus's murrelet nest occupancy rates for occupied nests, Cat Canyon, Santa Barbara Island, 1983–2002.

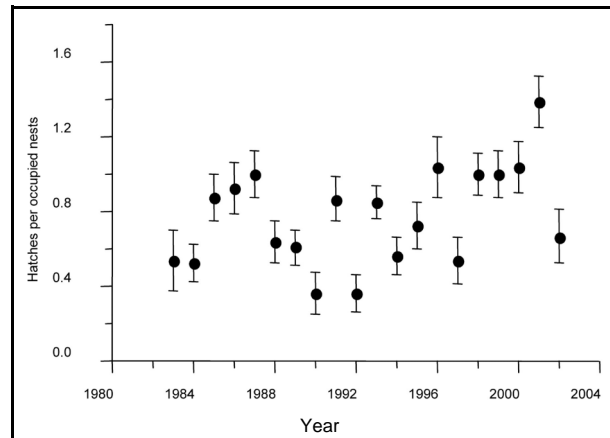


Figure 2. Mean number of eggs hatched from occupied nests, Cat Canyon, Santa Barbara Island, 1983 – 2002.

period was positively correlated with the mean number of eggs hatched when the nest was occupied (Pearson correlation: $r = 0.46$, $n = 64$ nests, $P < 0.0001$). Thus, those nest sites that were used most often also produced the most hatched eggs when occupied (Fig. 7).

Nest Success and Elevation

On average, nests were located 35.7 ± 8.5 m above sea level. Mean nest occupancy rates during the 20-year period were not correlated with the nest's elevation (Pearson correlation: $r = 0.05$, $n = 52$ nests, $P = 0.71$). Similarly, the mean number of eggs hatching when a nest was occupied (Pearson correlation: $r = 0.06$, $n = 52$ nests, $P = 0.67$) and the total number of eggs hatching from a nest

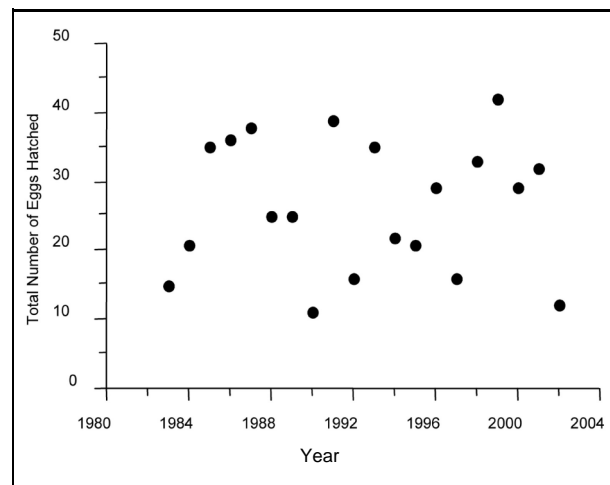


Figure 3. Total number of Xantus's murrelet eggs hatched, 64 nests, Cat Canyon, Santa Barbara Island, 1983–2002.

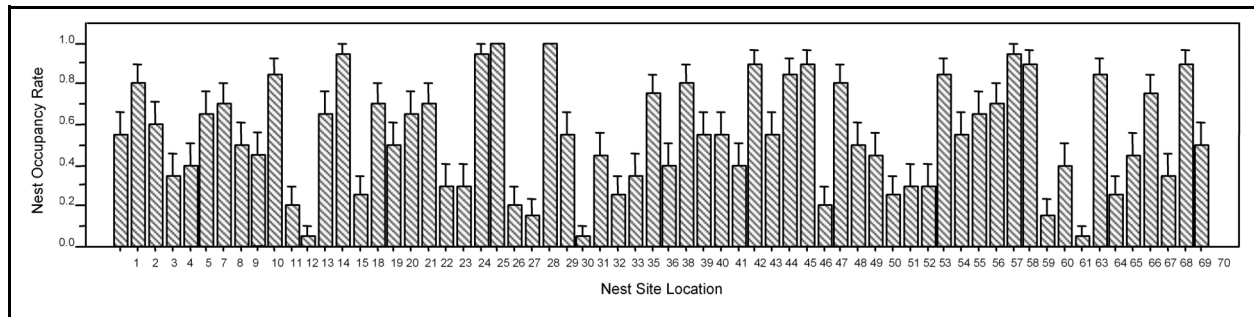


Figure 4. Nest occupancy rate for 64 Xantus's murrelet nests, Cat Canyon, Santa Barbara, 1983–2002.

during the 20-year period (Pearson correlation: $r = 0.07$, $n = 52$ nests, $P = 0.63$) were not correlated with the nest's elevation.

Density-Dependent Nest Predation

From 1983–2002, the average density of occupied nests was 69.5 ± 15.1 nests hectare⁻¹. Nest success was not correlated to nest density among years (Pearson correlation: $r = 0.16$, $n = 20$ years, $P = 0.50$). We also investigated density-dependent effects at a smaller spatial scale by analyzing potential nearest-neighbor effects. For all years combined, nests were located 3.9 ± 4.7 m from the nearest neighboring nest; 16 of the 64 nests were located 1.0 m from another nest. Mean nest occupancy rates during the 20-year period were not correlated with nearest neighbor distance (Pearson correlation: $r = 0.14$, $n = 56$ nests, $P = 0.31$), nor were the mean number of eggs hatching when a nest was occupied (Pearson correlation: $r = 0.15$, $n = 56$ nests, $P = 0.29$) or the total number of eggs hatching from a nest during the 20-year period (Pearson correlation: $r = 0.15$, $n = 56$ nests, $P = 0.28$). We also found few nearest neighbor effects when we analyzed each year separately and used only those nests that were occupied each year

to calculate nearest neighbor distances. The fate of nests was not dependent on the distance to nearest neighbors in any year from 1983–2002 (Logistic regression: all Wald $\chi^2_1 \leq 2.39$, $17 \leq n \leq 41$ nests, $P \geq 0.12$), except in 1990 (Logistic regression: Wald $\chi^2_1 = 4.44$, $n = 25$ nests, $P = 0.04$) and 1998 (Logistic regression: Wald $\chi^2_1 = 3.05$, $n = 31$ nests, $P = 0.08$) when successful nests (1990: 6.9 ± 1.1 m; 1998: 6.7 ± 1.2 m) tended to be more highly spaced than unsuccessful nests (1990: 3.4 ± 0.5 m; 1998: 1.8 ± 0.5 m).

DISCUSSION

Our results indicate that although annual rates of nest occupancy by Xantus's murrelets at Cat Canyon are declining, as has been previously reported, this trend has not been accompanied by a reduction in annual productivity because nest success within the colony has increased since 1983. The resulting situation has been an average production of 27 murrelet chicks from the Cat Canyon breeding colony each year. While this is a relatively small number of birds, the number of occupied nests producing at least one chick each

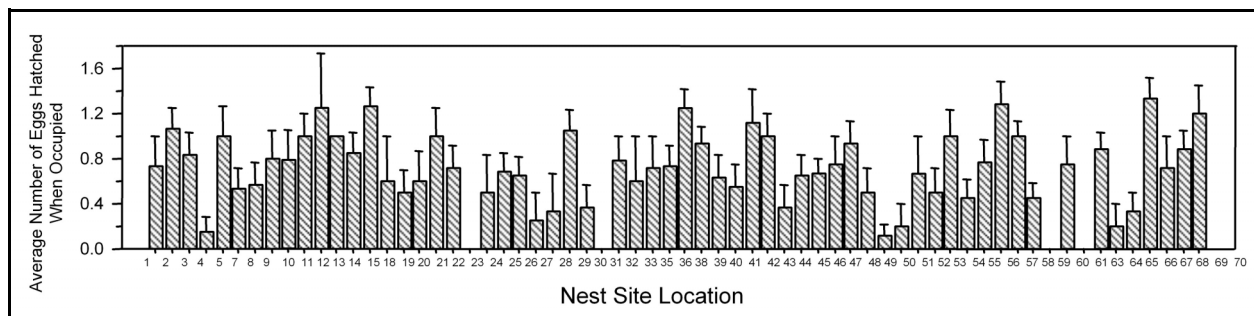


Figure 5. Average number of eggs hatched when a nest was occupied for 64 Xantus's murrelet nests, 1983–2002, Cat Canyon, Santa Barbara Island.

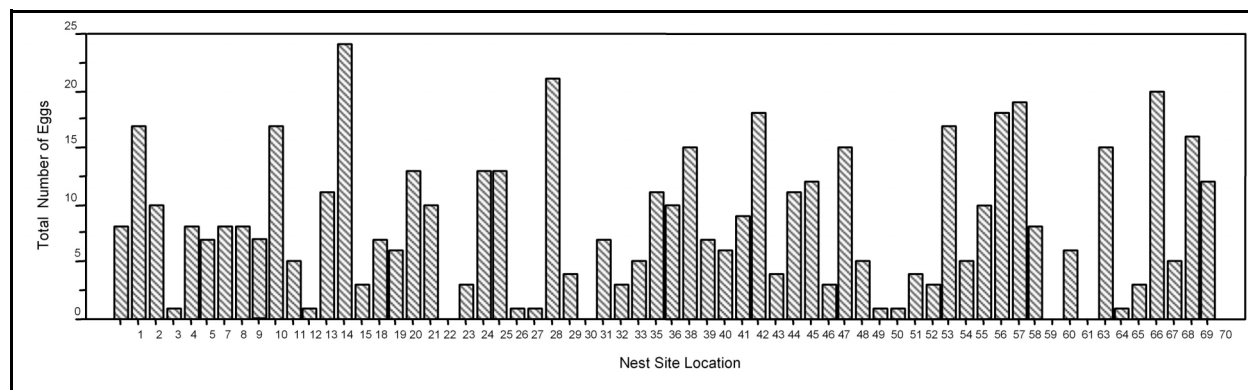


Figure 6. Total number of eggs hatched at each of 64 Xantus's murrelet nests, 1983–2002, Cat Canyon, Santa Barbara Island.

year is consistent with historical observations; our results show an average nest success rate over the 20-year period of 0.58 ± 0.17 (Fig. 2), whereas Drost and Lewis (1995) reported 57% nest success as summarized from all records to that time.

The reduction in nest density within the colony resulting from fewer nesting attempts had no observable effect on nest success. Many studies of colonial nesting seabirds have demonstrated that higher nest densities result in decreased rates of nest predation (Goetmark and Andersson 1984, Gilchrist 1999), although many of these examples involve avian predators. Our results suggest that for burrow nesters, such as Xantus's murrelets, nesting near conspecifics in order to benefit from shared predator defense strategies may not be as advantageous as it is in open-nesting species, and that lowered colony density, like that observed for

murrelets on SBI during the past two decades, does not increase predation risk or reduce nest success.

Some observers have questioned the ability of *P. maniculatus* to break murrelet eggs. These eggs are quite large (approximately 54 x 36 mm; Drost and Lewis 1995) and previous studies of *P. maniculatus* have found this species unable to consume eggs of this size (Bradley and Marzluff 2003). As far as we know, no one has ever observed a mouse actually break open a Xantus's murrelet egg. However there is no other explanation we can think of for the high number of broken eggs found in murrelet burrows. Deer mice are the only mammals on SBI, and the only other vertebrate species present (the island night lizard, *Xantusia riversiana*) is far too small to consume eggs of this size (Fellers and Drost 1991). Most depredated eggs are found inside murrelet nesting crevices, eliminating the possibility that avian predators such as western gulls (*Larus occidentalis*) are the culprits (Drost and Lewis 1995).

We believe that the observed increase in individual murrelet nest success is due to a decrease in egg depredation by mice, and we suggest two possible causative mechanisms. First, land cover changes occurring on the island over the last two decades may be altering mouse behavior and distribution near the murrelet colony. Vegetation recovery since the removal of rabbits (*Oryctolagus cuniculus*) in 1981 has been slow but measurable, and has resulted in a greater abundance of several native plant species, specifically *Coreopsis gigantea* (Halvorson et al. 1997, Johnson and Rodriguez 2001, NPS unpubl. data). Monitoring data collected for deer mice

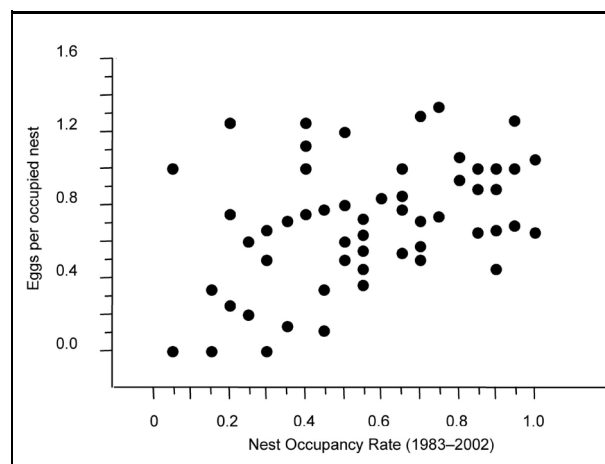


Figure 7. Number of Xantus's murrelet eggs hatched per nest occupancy rate, (occupied nests with hatched eggs, $n = 55$), 1983–2002, Cat Canyon, Santa Barbara Island.

during the same period show that mice are more numerous in native habitat areas on the island than in non-native ones (Schwemm and Coonan 2001, Schwemm and Martin 2005, NPS unpubl. data). The specific mechanisms that result in higher mouse densities in these areas are yet to be defined, however we suggest that greater food resources available in areas that also provide better cover, i.e., *Coreopsis* stands, encourage mice to forage more frequently in those areas as opposed to Cat Canyon, which has fewer shrubs and relatively less protection for mice from their primary predator, barn owls (*Tyto alba*; Kotler et al. 1991).

Secondly, rodent foraging patterns change with food availability and distribution (Brown 1988, Yunker et al. 2002). As egg density within the colony declines, search costs for mice increase, as do perceived predation risks (Lewis et al. 2001). Studies on songbird eggs have demonstrated that mice often take eggs only as incidental prey while foraging for other items (Vickery 1992, Schmidt et al. 2001), and this may also be the case for deer mice at Cat Canyon. Additional discussion of mouse population dynamics and murrelet nest success on SBI is included in Schwemm and Martin (2005).

Because we found no spatial explanations for variations in nest success, we speculate that the long-term likelihood that a particular nest will be successful may be determined in large part by individual quality. Xantus's murrelets are long-lived birds (Drost and Lewis 1995), with high nest site fidelity (Murray et al. 1983, Drost and Lewis 1995). These demographics suggest that successful nests might represent long-term occupation by successful pairs, and perhaps their offspring (Pyle et al. 2001). The mechanisms responsible for successful nesting by Xantus's murrelets are unknown, but might include greater nest attentiveness, increased aggression toward predators, greater foraging ability (resulting in less time away from the nest), and other intrinsic characteristics of individual birds. This hypothesis will be difficult to test, owing to the challenges of studying nesting murrelets, but we suggest that further research in this area is needed. Finally, differences in individual site attributes may also contribute to nest success. Nest attribute data were collected in 2001 for all known and potential nest sites on Santa Barbara Island, and when combined

with nest success data may illustrate nest attribute preferences for murrelets (D. Whitworth pers. comm.).

Egg predation occurs most often when adults are foraging away from the nest (Murray et al. 1983, Drost and Lewis 1995) or after nests have been abandoned. High numbers of Xantus's murrelet eggs are lost annually to abandonment (Drost and Lewis 1995, C. Phillips pers. comm.) and it is not generally known whether an egg was abandoned prior to depredation. Observer disturbance can cause egg neglect or abandonment, particularly if the disturbance occurs during early incubation (Burger and Gochfeld 1999, Bolduc and Guillemette 2003). We suggest however that observer impacts did not influence the negative trends in nest occupancy reported here. While disturbance at nest sites may affect some individuals, adult murrelets at the nest have not been handled for the last 20 years. Experienced researchers suggest that over time birds become somewhat habituated to observer presence (Burger and Gochfeld 1999, Whitworth pers. comm.), and those individuals that are the least affected by occasional disturbance may in fact be the birds occupying the most successful nests. We suggest that while observer presence in the colony likely does have some effect on individual birds, these impacts have not changed over the course of this study, and therefore are not responsible for the observed decline in nest occupancy rates.

Management Implications

Predation by native species on rare species presents managers with challenges for protection of the species at risk. Impacts to the rare species from natural predation must be evaluated in terms of costs, both economic and ecologic, of purposely manipulating the existing predator-prey relationship (Goodrich and Buskirk 1995). In the last few decades murrelets have lost nesting areas within their range to human use and non-native predators (McChesney and Tershey 1998, Pacific Seabird Group 2002), and threats to adult birds at-sea have apparently significantly reduced the population of breeding birds (Drost and Lewis 1995, Carter et al. 2000, Pacific Seabird Group 2002). Previous studies have indicated that nest occupancy has declined on the island over the last two decades (Burkett et al. 2003), and our results

confirm that analysis. However the relationship between murrelets and deer mice on Santa Barbara Island has evolved over thousands of years (Ashley and Wills 1987), and under natural conditions the two species were likely in balance (Burger and Gochfeld 1994).

There is no evidence to suggest that mouse populations on Santa Barbara Island are higher at present than they were historically, a condition that would suggest greater than normal predation pressures on murrelets (Schwemm and Martin 2005). The hypothesis that mouse numbers are anthropogenically inflated on the island has appeared repeatedly in the literature (Murray et al. 1983, D'Antonio et al. 1992, Drost and Lewis 1995, Halvorson et al. 1997, Sydeman et al. 1998), but has never been tested. Our results indicate that predation pressures on murrelets from mice have not increased over the past 20 years and, in fact, may be declining. Proposed large-scale efforts to control native mice at breeding sites will likely be labor-intensive (P. Stapp, pers. comm.), may invoke prey-switching that increases owl predation on adult murrelets (Ackerman 2002, Schmidt and Ostfeld 2003a), and may have additional undesired effects on island system function (Goodrich and Buskirk 1995). Targeted management of productive nests might afford a better alternative for murrelet recovery; nests that have high occupancy rates but high levels of egg loss could be selected for specific protection, while nests that are rarely occupied, regardless of nest outcome, would not warrant particular effort.

ACKNOWLEDGMENTS

We thank H. Carter, D. Whitworth, and R. Young for their persistence in data collection. Many others, including volunteers and seasonal staff for NPS and USGS, assisted with data collection and we are grateful for their dedication. C. Drost provided unending and consistently thought-provoking ideas regarding all things alive on Santa Barbara Island. Student Conservation Association interns and staff from Point Reyes Bird Observatory, Humboldt State University, and C. Phillips of U.C. Santa Cruz were consulted on biology of murrelets. P. Stapp and S. Millus shared preliminary results from their deer mouse research on Santa Barbara Island. We thank C. Ackerman for

GIS technical support and K. Phillips, A. Blackmer, J. Yee and M. Glassow for helpful comments on earlier drafts of the manuscript. Two anonymous reviewers provided critical input that greatly improved the paper. J.T. Ackerman was supported by the United States Geological Survey, Science Support Program for the Minerals Management Service, Pacific Outer Continental Shelf Region. GPS data were collected in 2001 as part of a separate study by Humboldt State University, California Institute of Environmental Studies, and Channel Islands National Park, with support from California Department of Fish and Game, U.S. Fish and Wildlife Service, U.S. Geological Survey, and U.S. Navy, and used with permission.

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