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Received 17 November 2005, accepted 18 January 2006

SUMMARY

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.

We report the first quantitative information on hatching success and assortative mating of Xantus's Murrelets *Synthliboramphus hypoleucus* in Mexico, obtained at the San Benito Islands, Baja California, during 2003 and 2004. The San Benito Islands are one of the southernmost murrelet colonies, do not have native Deer Mouse *Peromyscus maniculatus* egg predators, and support both murrelet subspecies. We compare murrelet breeding biology at San Benito Islands with that at the well-studied colony of Santa Barbara Island, California, near the northern end of the breeding range where Deer Mice are present. In 2003 and 2004, murrelets began laying eggs 3–6 weeks earlier on the San Benito Islands than at Santa Barbara Island. The mean number of eggs hatched per nest at the San Benito Islands was 0.55 ± 0.83 in 2003 and 0.72 ± 0.79 in 2004, significantly lower than at Santa Barbara Island in both years $(1.21 \pm 0.78 \text{ and } 1.11 \pm 0.94, respectively)$. Causes of hatching failure differed between colonies. Nest abandonment was most common at the San Benito Islands in both years. On Santa Barbara, mouse depredation was the largest cause of failure in 2003 and mouse depredation coupled with abandonment in 2004. Most breeding individuals at the San Benito Islands (62.5%) were *S. h. scrippsi*, 22.5% were *S. h. hypoleucus* and 15% were intermediates (n = 40). Based on facial patterns of 20 breeding pairs, most pairs (70%) were monotypic (11 *S. h. scrippsi* and 3 *S. h. hypoleucus*), but five pairs involving intermediates and one mixed pair indicated some interbreeding between subspecies. Long-term monitoring is needed at the San Benito Islands to further assess breeding success in the southern portion of the range and especially to investigate the effects of avian predators and variable prey availability.

Key words: Assortative mating, breeding biology, predation, Santa Barbara Island, San Benito Islands, *Synthliboramphus hypoleucus*, Xantus's Murrelet

INTRODUCTION

The Xantus's Murrelet Synthliboramphus hypoleucus is a small, diving alcid that is listed as Endangered in Mexico and Threatened in California because of its limited breeding range, small and declining global population size, and vulnerability to multiple threats (Drost & Lewis 1995, Burkett et al. 2003). The murrelet is thought to breed at 13 islands or island groups over 500 km between Point Conception, California, and Punta Abreojos, Baja California Sur (Drost & Lewis 1995, Carter et al. 2005, Keitt 2005). The global population is estimated at 5000-10000 breeding pairs, and the seven historic Mexican colonies (four with confirmed current breeding populations) are thought to support at least half of the worldwide population (Burkett et al. 2003, Karnovsky et al. 2005, Keitt 2005). Populations of the subspecies S. h. scrippsi are found at all colonies except Guadalupe Island. However, the nominate subspecies S. h. hypoleucus is limited mainly to the offshore islets of Guadalupe Island and the San Benito Islands, the only colony where it is known to overlap with S. h. scrippsi (Drost & Lewis 1995, Carter et al. 2005, Keitt 2005).

Breeding biology of Xantus's Murrelet is known primarily from studies since 1975 at Santa Barbara Island, California, where murrelets nest mainly in rock crevices and under vegetation on coastal slopes (Murray *et al.* 1983, Drost & Lewis 1995). Declines in Xantus's Murrelet population size and nest occupancy at Santa Barbara Island, and persistent on-colony and at-sea threats have raised concerns about the long-term viability of murrelet populations (Hunt *et al.* 1981, Carter *et al.* 1992, Drost & Lewis 1995, McChesney & Tershy 1998, Sydeman *et al.* 1998, Carter *et al.* 2000, Burkett *et al.* 2003, Whitworth *et al.* 2003a). Long-term monitoring at Santa Barbara Island has also indicated that Xantus's Murrelet productivity is low as compared with the congeneric Ancient Murrelet *Synthliboramphus antiquus* mainly because of high egg predation by Deer Mice *Peromyscus maniculatus* (Murray *et al.* 1979, Murray *et al.* 1983, Drost & Lewis 1995).

Given concerns about the Xantus's Murrelet population at Santa Barbara Island, we initiated a study of Xantus's Murrelet breeding biology at the San Benito Islands, Baja California, in 2003 and 2004 to determine whether hatching success differed substantially at a colony without native mice. Further goals were to compare timing of egg-laying and egg fates between the San Benito Islands and Santa Barbara Island. In addition, we examined the proportions of each subspecies and pairings between subspecies that bred at the San Benito Islands to assess the level of interbreeding between *S. h. scrippsi* and *S. h. hypoleucus*.

METHODS

Study area

The three San Benito Islands, totaling 6.4 km² in area, are located approximately 480 km south of the U.S.-Mexico border on the central west coast of Baja California (Fig. 1). West Island (28°18'N, 115°34'W), where our study was conducted, is the largest and highest of the islands (maximum elevation 216 m) with steep cliffs bordering the west and south shores. These islands are arid and sparsely vegetated with maritime desert scrub (Junak & Philbrick 2000). They are owned and governed by the Mexican federal government and are virtually unprotected (Wolf 2002). However, in 2005, a proposal to create a biosphere reserve to protect the San Benito Islands and six other islands or island groups in the region was submitted to the Mexican government and has been accepted and distributed for public comment. A seasonal fishing camp comprising approximately 35 buildings is operated by the cooperative Pescadores Nacionales de Abulón, and a lighthouse is staffed by one person year-round.

Xantus's Murrelets nest in rock crevices on all three San Benito Islands, although they were earlier noted nesting under Agave *Agave sebastiana* (Kaeding 1905). A.W. Anthony provided the earliest record of Xantus's Murrelets on the San Benito Islands, noting that murrelets were calling from the water during his July 1897 expedition (Anthony 1900). Kaeding (1905) reported Xantus's Murrelets as "fairly common on and about" the islands. DeLong & Crossin (1968) and Jehl & Bond (1975) captured murrelets at sea around the islands but gave no estimate of abundance. In 1999, Keitt (2005) used vocalization surveys and nest searches to estimate 300–750 breeding pairs on the three islands. Whitworth *et al.*

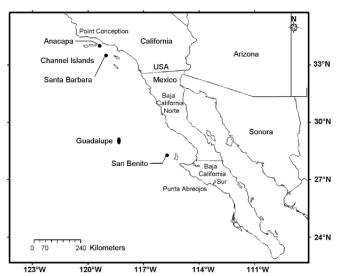


Fig. 1. Breeding range of Xantus's Murrelets from Point Conception, California, to Punta Abreojos, Baja California Sur, showing locations of Santa Barbara, San Benito, Anacapa and Guadalupe islands.

(2003b) conducted nocturnal spotlight surveys in March 2002 and tentatively estimated 250–500 breeding pairs on the three islands.

Although no native Deer Mice are present, native avian predators include hundreds of Common Ravens *Corvus corax*, small numbers of Barn Owls *Tyto alba*, at least two pairs of Peregrine Falcons *Falco peregrinus*, and approximately 500 pairs of Western Gulls *Larus occidentalis* (S. Wolf, unpubl. data 2000, 2001). Rabbits *Oryctolagus cuniculus*, which may have competed with murrelets for nest sites, were introduced in the 1990s but were eradicated in 1998 from the West and Middle Islands (Donlan *et al.* 1999) and in 2001 from East Island. Feral cats *Felis catus* were abundant in the 1920s but have not been detected since the early 1990s (McChesney & Tershy 1998).

Twelve breeding seabird species and subspecies inhabit the San Benito Islands, including important populations of Black-vented Shearwater *Puffinus opisthomelas*, Black Storm-Petrel *Oceanodroma melania*, Leach's Storm-Petrel *O. leucorhoa chapmani*, Least Storm-Petrel *O. microsoma*, and Cassin's Auklet *Ptychoramphus aleuticus* (Wolf 2002). Based on at-sea captures, Craveri's Murrelet *Synthliboramphus craveri*, a close relative of Xantus's Murrelet, has been presumed to nest on the San Benito Islands (DeLong & Crossin 1968). However, active nests of Craveri's Murrelet have not been documented in the past at the San Benito Islands (Keitt 2005) and were not detected in this study.

Nest monitoring

Two nest monitoring plots were established on the north coast of West Island in January 2003 (Fig. 2) in areas where we found moderate-to-high densities of murrelet nests during comprehensive nest searches conducted in April 2000. We marked plot perimeters with a handheld Garmin global positioning system unit (Garmin International, Olathe, KS, USA). Within plot boundaries, we monitored all potential nest sites that contained murrelet eggshell remnants from prior years or where crevice dimensions provided suitable nesting habitat. Our searches resulted in 94 monitored sites in the Red Rocks plot, including five sites added opportunistically in March–April 2003, and 12 monitored sites in the White Rocks plot, including one site added opportunistically in March 2003.

Timing of egg-laying and hatching success

In 2003 and 2004, all sites were checked for occupancy and status every five days beginning in mid-January before egg-laying and ending in early June when nesting activity had completely ended. To prevent possible researcher impacts through abandonment or damaging eggs, we did not handle or band murrelets at their nest sites (Murray *et al.* 1983). The presence of birds and eggs was noted

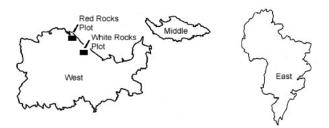


Fig. 2. Location of Red Rocks and White Rocks study plots on West San Benito Island. (Map reproduced with permission from Pronatura Noroeste [1998].)

on each check date. When unattended eggs were found in a site, we numbered them with a felt marker, measured length and width using Vernier calipers, and returned them in the same position as found. After adults and chicks left a nest site, we collected the eggshells to determine clutch size and egg fates. The shells of hatched eggs have dry, papery membranes that are often separated from the shell and lined with blood vessels. The shells of eggs that have been broken have shiny, adherent membranes that often show traces of yolk. These same eggshell characteristics are used for assessing hatching success and clutch size at Santa Barbara and Anacapa Islands (Wolf *et al.* 2000, Whitworth *et al.* 2005). At some nests, we could not determine egg fates or confirm clutch size if eggshell remnants were not found.

Hatching success was calculated by two methods for comparison with measures used in murrelet studies at Santa Barbara and Anacapa (Whitworth *et al.* 2005) islands. The mean number of eggs hatched per nest was calculated as the total number of hatched eggs (excluding dead chicks) divided by the total number of active nest sites (comparable to "productivity" measured at Santa Barbara Island). The percent of nests that hatched was calculated as the percent of active nest sites that successfully hatched at least one egg (used by Whitworth *et al.* [2005] at Anacapa Island).

Subspecies pairings

Facial plumage patterns of breeding pairs were scored using criteria and illustrations in Jehl & Bond (1975). We assigned birds with facial patterns 3 or 4 as *S. h. scrippsi*, facial pattern 2 as an intermediate form, and facial patterns 0 or 1 as *S. h. hypoleucus* (after Jehl & Bond 1975). Once an adult was found at a site, we scored its facial pattern each day until a distinctly new facial pattern was observed or for a maximum of ten days, including any days

San Benito 2003

when eggs were left unattended. In 2004, we reduced visitation for scoring facial patterns to every other day until a new pattern was observed or for a maximum of 10 days. To avoid disturbing incubating adults, we examined facial patterns only in sites where viewing could be accomplished quickly and easily.

Comparison with Santa Barbara Island

We used nest monitoring data from the Cat Canyon plot at Santa Barbara Island because most nest sites in that plot are in rock crevices rather than under vegetation, similar to those at the San Benito Islands. Nest monitoring methods at Santa Barbara Island are comparable to methods used in this study.

RESULTS

Timing of egg-laying and hatching success

We found 29 active nest sites in 2003 in the two West Island plots combined and 25 active sites in 2004 in the Red Rocks plot only. In 2003, laying of the first egg began on 13 March, peaked in late March ($\overline{X} = 29$ March), and ended on 7 May (n = 24). In 2004, laying of the first egg (Fig. 3) began on 26 January, peaked in February through early March ($\overline{X} = 28$ Feb) and ended on 22 April (n = 24). The mean number of eggs hatched per nest was 0.55 ± 0.83 (n = 29) in 2003 and 0.72 ± 0.79 (n = 25) in 2004, which was not significantly different ($\chi^2 = 0.12$, df = 1, *P* = 0.73). The percent of nests that hatched was 35% (10/29) in 2003 and 52% (13/25) in 2004. Mean clutch size was 1.70 ± 0.54 eggs (n = 30 nest attempts) in 2003 and 1.86 ± 0.52 eggs (n = 28 nest attempts) in 2004. However, at 10 sites in 2003 and six sites in 2004 where we found evidence of a one-egg clutch, we could not be certain that a second egg did not disappear undetected.



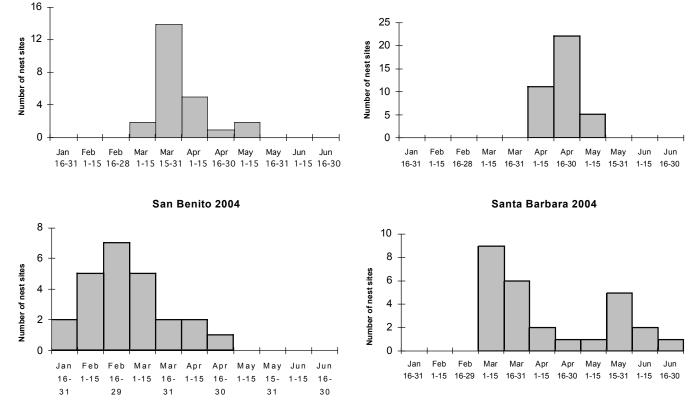


Fig. 3. Timing of clutch initiation on West San Benito Island and Santa Barbara Island in 2003 and 2004.

Of 51 eggs laid in 2003 (Table 1), most were abandoned (47%), hatched (31%) or disappeared (14%). Of 52 eggs laid in 2004 (Table 1), most hatched (35%), were abandoned (27%), never hatched (19%) or disappeared (16%). Abandonment accounted for 69% of 35 failed eggs in 2003 and 41% of 34 failed eggs in 2004. In 2003, adults at 64% (9/14) of abandoned nest sites appeared to abandon before incubation, because we never observed adults. Likewise in 2004, adults at 25% (2/8) of abandoned sites appeared to abandon before incubation.

Subspecies pairings

We confirmed subspecies identities for both pair members of eight breeding pairs in 2003 and 12 breeding pairs in 2004. Two confirmed pairs in 2003 nested outside of monitoring plots under structures in the fishing camp. All confirmed pairs in 2004 were nesting in sites different than those confirmed in 2003, and we assumed that they were different birds. Assortative mating occurred in 14 pairs: 11 were *scrippsi* pairs and three were *hypoleucus* pairs. The remaining six pairs were non-assortative: two were pairs of an intermediate with *scrippsi*, two were pairs of an intermediate with *hypoleucus*, one was a pair of two intermediates and one was a mixed pair (i.e. *scrippsi* paired with *hypoleucus*).

We found no evidence for differences in timing of breeding among monotypic, intermediate and mixed pairs, although we found possible evidence for differences in hatching success. In 2003, the percentage of nests that hatched was 100% (3/3) for *scrippsi* pairs, 100% (1/1) for the intermediate × intermediate pair, and 0% (0/2) for *hypoleucus* pairs. In 2004, the percentage of nests that hatched eggs was 86% (6/7) for *scrippsi* pairs, 25% (1/4) for the intermediate × one subspecies pairs, and 100% (1/1) for the mixed *scrippsi* × *hypoleucus* pair.

Comparison with Santa Barbara Island

At Santa Barbara Island, 42 active nest sites were found in the Cat Canyon nest monitoring plot in 2003 and 40 active sites were found in 2004, although three of these active sites were excluded from analysis because of unclear egg fates. First egg dates (Fig. 3) ranged from 4 April to 14 May ($\overline{X} = 19$ April) in 2003 (n = 38) and 5 March to 21 June ($\overline{X} = 15$ April) in 2004 (n = 27). The mean number of eggs hatched per nest was 1.21 ± 0.78 (n = 42) in 2003 and 1.11 ± 0.94 (n = 37) in 2004. Hatching success at Santa Barbara Island was significantly higher than at the San Benito Islands in

 TABLE 1

 Fate of eggs laid at West San Benito Island

 and Santa Barbara Island in 2003 and 2004

	San Benito		Santa Barbara	
	2003	2004	2003	2004
Hatched	16	18	51	41
Depredated	0	0	12	11
Cracked	3	3	0	2
Disappeared	7	5	3	2
Abandoned	24	14	3	13
Never hatched	1	10	4	2
Dead chick at hatch	0	2	1	1
Unknown	0	0	1	1
TOTAL	51	52	75	73

both 2003 ($\chi^2 = 16.36$, df = 1, P < 0.001) and 2004 ($\chi^2 = 5.66$, df = 1, P = 0.017). The percentage of nests that hatched was 81% (34/42) in 2003 and 68% (25/37) in 2004. Causes of egg failure differed between the two islands. The largest cause of egg failure on Santa Barbara Island in 2003 was mouse depredation, which affected 50% of 24 failed eggs; in 2004, mouse depredation and egg abandonment affected 34% and 41% of 32 failed eggs, respectively (Table 1). Egg abandonment at the San Benito Islands was significantly higher than at Santa Barbara Island ($\chi^2 = 18.03$, df = 1, P < 0.001) in 2003, but not in 2004 ($\chi^2 = 0.002$, df = 1, P = 0.96).

DISCUSSION

At the San Benito Islands as compared with Santa Barbara Island, Xantus's Murrelet egg-laying was earlier and hatching success was significantly lower in 2003 and 2004, suggesting that different mechanisms may affect productivity at the two colonies. In both years, murrelets began laying eggs three to six weeks earlier at the San Benito Islands than at Santa Barbara Island, and egg dates were four to six weeks later at both colonies in 2003 as compared with 2004.

Timing of breeding of alcids in California is related to prey availability within the California Current Upwelling System and is strongly influenced by oceanographic conditions (Ainley & Boekelheide 1990). Xantus's Murrelets prey mainly on larval and juvenile fish and euphausiids (Hamilton *et al.* 2004), and delayed egg-laying has been linked to low prey abundance and poor oceanographic conditions in their foraging areas (Hunt & Butler 1980). At Santa Barbara Island, Xantus's Murrelets are quite variable in their timing of breeding, with laying occurring as early as February and as late as July (Hunt & Butler 1980; Murray *et al.* 1983; Drost & Lewis 1995; P. Martin, unpubl. data).

Earlier egg-laying at the San Benito Islands suggests that prey availability in foraging areas, mainly within Vizcaino Bay, occurred earlier than in foraging areas within the Southern California Bight used by murrelets breeding at Santa Barbara Island. Later egg-laying observed in 2003 at both colonies was likely related to delayed prey availability during the weak El Niño event in the California Current System that peaked in winter 2002/03 and dissipated rapidly in April 2003 (Venrick *et al.* 2003).

Our data from 2004 and opportunistic observations in 1999 and 2001 (Keitt 2005; S. Wolf, unpubl. data) indicate that murrelets at the San Benito Islands begin egg-laying in January in some years. Previously, the earliest known egg date (excluding abandoned eggs) at the San Benito Islands was 9 March 1899 and the latest was 25 June 1968 (Drost & Lewis 1995, Whitworth *et al.* 2003b). To our knowledge, prior earliest egg dates recorded at any murrelet colony were mid-to-late February at Santa Barbara Island (Drost & Lewis 1995, Wolf *et al.* 2000). Because the range of dates of known egg-laying derives largely from sporadic collecting trips biased toward later months (Drost & Lewis 1995), more complete studies may reveal earlier egg dates at other colonies.

We expected that Xantus's Murrelets would experience higher hatching success at the San Benito Islands than at Santa Barbara Island because of the absence of Deer Mice. However, hatching success per nest was significantly lower on the San Benito Islands than on Santa Barbara Island in both years, largely because of relatively high rates of egg abandonment (41%–60% of failed eggs) at the San Benito Islands as compared with Santa Barbara Island,

and relatively low rates of egg depredation by mice (15%-16%) of eggs laid) at Santa Barbara Island as compared with other years (Drost & Lewis 1995). Between 1993 and 1999, egg depredation averaged 72% of failed eggs (range: 57%–83%) in the Cat Canyon study plot at Santa Barbara Island (Martin & Sydeman 1998, Roth *et al.* 1998, Roth *et al.* 1999, Wolf *et al.* 2000), compared with 50% and 34% in 2003 and 2004 respectively.

Three potential explanations for high egg abandonment at the San Benito Islands are researcher disturbance, depredation of adults, and reduced prey availability. We visited nests more frequently than at Santa Barbara Island to observe facial patterns of nesting birds, thereby creating a higher potential for disturbance. However, in both years, a large percentage of birds (25%-64%) abandoned their nests before we observed them, suggesting that researcher disturbance was not the cause. Common Ravens, Barn Owls, Peregrine Falcons and Western Gulls have been documented to prey upon Xantus's Murrelet adults at the San Benito Islands (S. Wolf, unpubl. data). In 2003, we frequently noted tens of Common Ravens in the Red Rocks study plot and adjacent nesting habitat, and found a depredated murrelet, raven feathers, and yolk remains outside one abandoned study site. In both years, we noted murrelet remains in tens of Barn Owl pellets in the Red Rocks plot. On Santa Barbara Island, heavy murrelet predation by Barn Owls (up to 10% of the nesting population) has been documented in some years, highlighting the significance of avian predators (Drost & Lewis 1995, Wolf et al. 2000). Overall, depredation of adults likely contributed to high nest abandonment at the San Benito Islands.

The weak El Niño in winter 2002/03 may also have contributed to high egg abandonment at the San Benito Islands in 2003 by lowering murrelet prey availability. At the Farallon Islands in central California, for example, the productivity of most seabird species declined in 2003 as compared with 2002 and 2004, which was attributed to El Niño oceanographic conditions (Goericke et al. 2005). However, murrelet hatching success was notably high in 2003 at Santa Barbara and Anacapa Islands. At Santa Barbara Island, mean number of eggs hatched per nest between 1990-1999 in the Cat Canyon plot was 0.73 ± 0.22 (range: 0.37–1.03; Ingram 1992, Ingram & Jory-Carter 1997, Martin & Sydeman 1998, Roth et al. 1998, Roth et al. 1999, Wolf et al. 2000), indicating that 2003 (1.21 ± 0.78) was well above average. The percent of nests that hatched in 2003 was 81% at Santa Barbara Island and 80% (12/15) at Anacapa Island (Whitworth et al. 2005), compared with 35% at the San Benito Islands. Therefore, El Niño conditions in 2003 may have had a lesser effect on murrelet prey availability in the Southern California Bight than in Vizcaino Bay.

Our study is the first to report proportions of nesting individuals and nesting pairs on the San Benito Islands that belong to each subspecies or the intermediate form. Earlier studies of murrelets at the San Benito Islands have indicated that a high proportion (40%– 61%) of Xantus's Murrelets captured from at-sea congregations belonged to the *S. h. scrippsi* subspecies (Jehl & Bond 1975, Whitworth *et al.* 2003b, Keitt 2005). These studies also reported significant morphologic differences between subspecies and a low abundance of intermediate forms, suggesting that nonrandom mating was maintaining subspecies in sympatry (Jehl & Bond 1975, Whitworth *et al.* 2003b). Both Whitworth *et al.* (2003b) and Jehl & Bond (1975) found that *S. h. hypoleucus* exhibits a significantly longer culmen, shallower bill depth, shorter tarsus and lower weight than *S. h. scrippsi*. We found that 62.5% of 40 nesting individuals were *scrippsi* (similar to 61% determined from at-sea captures in 2002; Whitworth *et al.* 2003b), 22.5% were *hypoleucus* and 15% were intermediates. We also found a high incidence (70%) of pairs with both members belonging to the same subspecies, indicating that some isolating mechanism is reducing interbreeding between subspecies. However, the presence of intermediate forms and non-assortative matings indicate that substantial hybridization is occurring between subspecies at the San Benito Islands. No evidence of differences in timing of breeding between subspecies was found. However, our small sample size suggests that monotypic *scrippsi* pairs may have higher hatching success than intermediate pairs, indicative of a potential isolating mechanism.

The presence of the nominate *hypoleucus* subspecies at the San Benito Islands may reflect movements of murrelets from Guadalupe Island, where nesting has become restricted to offshore islets without introduced predators (Green & Arnold 1939, Keitt 2005). Timing of breeding is similar at San Benito and Guadalupe Islands, facilitating such movements (Keitt 2005). We speculate that the *hypoleucus* population at the San Benito Islands may be sustained in part by movements of birds from Guadalupe Island, but that their progeny raised at the San Benitos may interbreed freely with *scrippsi*. Clearly, more work is needed to understand the mechanisms of interbreeding between the subspecies.

Important differences between colonies in timing of breeding, hatching success, predation levels and subspecies emphasize the importance of monitoring multiple populations of Xantus's Murrelet to understand population trends, viability and threats to murrelets across their breeding range. Over our two-year study period, the San Benito Islands population hatched half as many chicks as the Santa Barbara Island population despite the lack of egg predators on the San Benito Islands. Further work is needed to examine the causes for high rates of abandonment at the San Benito Islands, including effects from avian predators and variable prey availability.

ACKNOWLEDGMENTS

We would like to thank Island Conservation, Grupo de Ecología y Conservación de Islas, and the fishing cooperative Pescadores Nacionales de Abulón for providing logistic support and transportation to the San Benito Islands. Funding was generously provided to S. Wolf in part by a NSF Graduate Student Fellowship and by PRBO Conservation Science. The Mexican government kindly granted the permits to work on San Benito Islands (Oficio Num/SGPA/DGVS/5283 from Secretaría de Medio Ambiente y Recursos Naturales and Ofício No. DCPEFM/211/2608/02 from Secretaría de Gobernación). Harry Carter and Esther Burkett provided helpful comments on the manuscript.

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