

SYMPOSIUM

BIOLOGY AND CONSERVATION OF XANTUS'S MURRELET

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Xantus's Murrelet chicks shortly before nest departure at Lava Bench, Cave #1, Anacapa Island, California, 28 May 2004 (Photo by D.L. Whitworth).

BIOLOGY AND CONSERVATION OF XANTUS'S MURRELET: DISCOVERY, TAXONOMY AND DISTRIBUTION

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SUMMARY

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The biology of Xantus's Murrelets *Synthliboramphus hypoleucus* is similar in many respects to better-studied Ancient Murrelets *S. antiquus*, especially regarding morphology and the species' precocial mode of post-hatching development. It nests mainly in rock crevices but also under shrubs on islands in southern California, United States, and northwestern Baja California, Mexico (27°N to 34°N). The species was discovered in 1859 by János Xántus. Two subspecies (*S. h. hypoleucus* and *S. h. scrippsii*) are recognized that show limited evidence of interbreeding. At sea, closely related Craveri's Murrelets *S. craveri* co-occur with Xantus's Murrelets off California and western Baja California during half the year, but the former species has a discrete breeding range in the Gulf of California, Mexico. Breeding was documented at 13 island groups between 1863 and 1976. Post-breeding dispersal as far north as central British Columbia, Canada (c. 52°N) was observed in the 1940s to 1960s. A few Xantus's Murrelets disperse south of breeding colonies to Magdalena Bay, Baja California (c. 24°N). The southernmost record is the type specimen collected by Xántus near Cabo San Lucas, Baja California (c. 23°N). Chief threats to this species include introduced mammalian predators on breeding islands, heightened predation by natural predators in human-modified island habitats, and oil pollution. In January 2005, a Pacific Seabird Group special symposium, "Biology and conservation of the Xantus's Murrelet," highlighted conservation concerns and promoted publication of recent studies of this little-known alcid, with nine symposium papers published in this issue of *Marine Ornithology*. Much of what we know about Xantus's Murrelets has been learned in recent years, and many aspects of biology remain to be described.

Key words: Xantus's Murrelet, *Synthliboramphus hypoleucus*, Craveri's Murrelet, *Synthliboramphus craveri*, distribution, taxonomy, genus *Endomychura*

INTRODUCTION

Xantus's Murrelet *Synthliboramphus hypoleucus* is one of four *Synthliboramphus* murrelets, which are unusual among marine birds for their precocial mode of post-hatching development (Sealy 1973, 1976; Murray *et al.* 1983; Gaston 1992; Drost & Lewis 1995; Gaston & Jones 1998). About two days after hatching, one or two well-developed chicks (Fig. 1) leave their nest site at night. They complete their development at sea where they are cared for by one or both parents for an unknown period of time. Most modern knowledge of the breeding biology of Xantus's Murrelet stems from one study at Santa Barbara Island, California, United States, in 1975–1977 (Murray *et al.* 1983) and nest monitoring there each year since 1985 (Drost & Lewis 1995). Early observations on breeding were made primarily at the Coronado Islands, Baja California, Mexico (e.g. Lamb 1909, Howell 1910).

Synthliboramphus murrelets have the most southern distribution of all alcids. Ancient Murrelets *S. antiquus* breed widely across the North Pacific, but Japanese Murrelets *S. wumizusume* are limited to Japan and Korea (Udvardy 1963, Springer *et al.* 1993, Gaston & Jones 1998). Xantus's and closely related Craveri's *S. craveri* murrelets breed only in southern California, northwestern Baja California and the Gulf of California. Within breeding ranges

of Xantus's, Craveri's, and Japanese murrelets, few or no other alcids coexist on colonies or at sea. Cool ocean conditions occur in southern California and northwestern Baja California during the relatively early breeding season of Xantus's Murrelets. These conditions provide marine habitat similar to more northerly habitats



Fig. 1. Precocial Xantus's Murrelet chicks shortly before nest departure at Lava Bench Cave #1, Anacapa Island, California, 28 May 2004. (Photo by D.L. Whitworth)

favored by other alcids (Gaston & Jones 1998). During the non-breeding season, individuals disperse offshore and northward, with most of the world population occurring north of the breeding range from central California to central British Columbia in late summer and early fall (Whitworth *et al.* 2000, Karnovsky *et al.* 2005).

In many ways, the biology of Xantus's Murrelet is similar to the better-known Ancient Murrelet (Storer 1945a, 1945b; Gaston & Jones 1998). In addition to nocturnal colony visitation, breeding on southern islands is facilitated by use of natural crevices, small caves, and hollows under shrubs for nesting cover, often on steep slopes or cliffs which are relatively inaccessible to researchers. Adaptations for feeding on planktonic fish and invertebrates at relatively shallow depths in offshore habitats (Hamilton *et al.* 2004, 2005) include multi-day incubation shifts and egg neglect (Murray *et al.* 1983, Drost & Lewis 1995, Whitworth *et al.* 2000, Roth *et al.* 2005). Access to offshore areas is facilitated by the use of offshore nesting islands and a generally narrow continental shelf. The striking black-and-white plumage is present year-round and does not appear to differ with age; prebasic molt occurs in late summer and a partial prealternate molt likely occurs in late winter (Drost & Lewis 1995).

Xantus's Murrelet was described less than 150 years ago, and the earliest images were photographs of a chick (Howell 1910) and adults

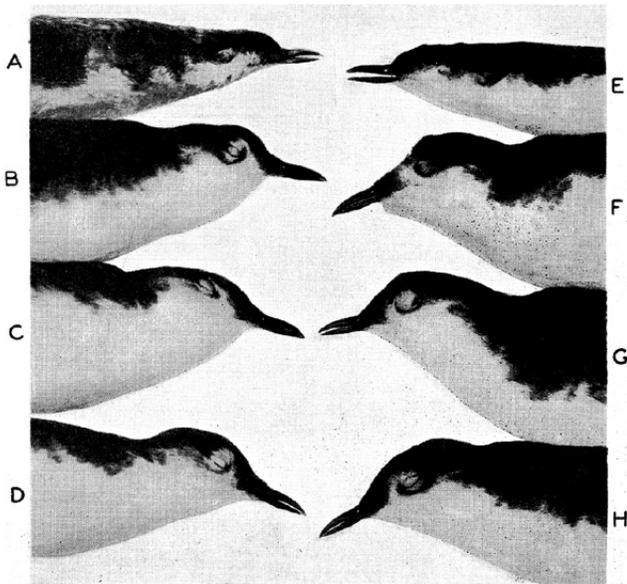


Fig. 2. "Murrelets showing characteristic white 'eye-area' of Xantus' type: A. 13046, U.S.N.M. [National Museum of Natural History, Smithsonian Institution, formerly the United States National Museum], female, type of *Endomychura hypoleuca* (Xantus), 14 miles off coast of Cape San Lucas, Lower California, Mexico, July 14, 1859 (from a photograph); B. 28057, C.A.S. [California Academy of Sciences], male, Guadalupe I., Lower Calif., April 19, 1925; C. 28056, C.A.S., male, Guadalupe I., Lower Calif., April 19, 1925; D. Collection Ed. N. Harrison, Encinitas, Calif., female, Guadalupe I., Lower Calif., April 6, 1938; E. 66618, U.S.N.M., female, San Jose, Lower Calif., March 1860, J. Xantus coll.; F. 38, S.D.S.N.H. [San Diego Society of Natural History], male, Guadalupe I., Lower Calif., May 18, 1892; G. 8867, S.D.S.N.H., male, Guadalupe I., Lower Calif., July 13, 1923; H. 17668, S.D.S.N.H., female, Guadalupe Is., Lower Calif., July 13, 1937". (Figure and caption reproduced with permission from Green & Arnold 1939: Fig. 14, copyright Cooper Ornithological Society)

(Van Rossem 1915). To help link recent studies with past knowledge, we provide historical and geographic information on the discovery of the species, taxonomy, and distribution that is not available in recent species accounts (Drost & Lewis 1995, Gaston & Jones 1998).

SPECIES DISCOVERY

Xantus's Murrelet was scientifically recognized in 1859, based on a specimen collected 14 miles (23 km) off the coast of Cabo San Lucas, Baja California, Mexico, on 14 July 1859 by János Xántus de Csisk Tapolsza, also known as John Xántus, Louis de Vésey, or Xántus de Vésey (Xántus 1859, Baird 1859, Zwinger 1986a; USNM #A13046, Fig. 2). Xántus also obtained a second specimen in March 1860 off nearby San José del Cabo (USNM #066618, Fig. 2), but both localities are far south of where Xantus's Murrelets have since been found to occur at sea (Brewster 1902). Xántus clearly documented collection dates and localities on specimen tags, and he mentioned the first specimen in a letter to S.F. Baird dated 23 July 1859, calling it a "*Phaleris*" species, using an old alcid genus name for auklets and puffins (Ridgway 1919, Zwinger 1986a). Both individuals apparently had dispersed far south of breeding colonies in the non-breeding season.

Along with A.L. Heermann, W. Gambel, and J.G. Cooper, Xántus (1825–1894) is recognized as one of the great early bird collectors in California and Baja California (Zwinger 1986a, 1986b; Fischer 2001). His name (Xántus or de Vésey) is also associated with two other birds (Xantus's Screech Owl *Otus asio xantusi* and Xantus's Hummingbird *Hylocharis xantusii*; AOU 1957) and many reptiles, mollusks, insects and plants. His discovery of *Synthliboramphus hypoleucus* carries some ornithological significance. Craveri's Murrelet was described subsequently in 1865, but its type specimen had been collected a few years earlier (1856 or 1857—Ridgway 1919, Violani & Boano 1990). The Long-billed Murrelet *Brachyramphus perdix* was reassigned species status in 1997 (Friesen *et al.* 1996), but had been originally described as a species in 1826 (Ridgway 1919). Thus, Xántus's collection of the murrelet bearing his name marked the last discovery of an extant alcid "new to science."

NOMENCLATURE AND TAXONOMY

Xantus's Murrelet has been called variously the White-bellied Murrelet (or Auk), Southern Auk, Xantus' Guillemot, Guadalupe Murrelet, or Scripps Murrelet (Grinnell & Miller 1944). In Spanish, it has been known as *Paloma del Mar* (as noted by Xántus in 1860; see Zwinger 1986a: 304), *Pato de noche* (Wilbur 1987), *Pato nocturno de Xantus* or *Pato nocturno de Scripps* (Drost & Lewis 1995), and *Mérgulo de Xantus* (Howell & Webb 1995). Ridgway (1919) summarized early taxonomy, and Coues (1903) and Ridgway (1896, 1919) described morphology and plumage in detail. After original description, the genus *Brachyramphus* was used from 1859 to 1909. From 1898 to 1900, the genus *Micruria* was applied, then *Endomychura* in 1899, which remained in use until 1983. This new genus contained only Xantus's and Craveri's murrelets, acknowledging these species' morphologic and geographic differences from *Brachyramphus* murrelets and other alcids. In 1944, the American Ornithologists' Union (AOU) chose to relump *Endomychura* with *Brachyramphus*, whereupon Storer (1945a, 1945b) demonstrated that *Endomychura* murrelets most closely resembled *Synthliboramphus* murrelets on most points of morphologic comparison (i.e. skull, pelvis, tarsometatarsus, wing length, plumage and eggs) and available ecological data. Bill

shape resembled *Brachyramphus* murrelets more closely, but was considered a less modified character. While examining the validity of using *Endomychura*, Storer (1945a) remarked:

Endomychura appears to be the most primitive genus of the Alcidae.... *Synthliboramphus* is an offshoot of this genus.... The relationship between *Endomychura* and *Synthliboramphus* parallels that between *Ptychoramphus* and *Aethia* or *Cyclorrhynchus*. In each case the more primitive genus (*Endomychura* or *Ptychoramphus*) agrees with the more advanced (*Synthliboramphus* or *Aethia* or *Cyclorrhynchus*) in skeletal structure and eggs, and differs in having a less deepened bill, in lacking elongated plumes on the head, and in having a more southern distribution.... Combination of the genera *Endomychura* and *Synthliboramphus* is a borderline case which "splitters" could never attempt to propose and which "lumpers" would jump to make. The gap between these two genera is so distinct that each name suggests a definite series of characters applicable to the two species of each genus.

Storer's careful work kept *Endomychura* in use long after 1945, but the genus *Synthliboramphus* was assigned in 1983 by the AOU (1983) for undocumented reasons.

The species name has been more consistent: *hypoleucus* from 1859, *hypoleuca* in 1898, then back to *hypoleucus* in 1983 (Ridgway 1919, AOU 1983). The English name, Xantus' Murrelet, was widely used after 1859, but was changed to Xantus's Murrelet in 1998 (AOU 1998).

Green & Arnold (1939) documented the existence of two subspecies with distinct plumages: *E. h. hypoleucus* (Guadalupe Island, which included the two specimens collected by Xantus), with extensive white in front and above the eye, and *E. h. scrippsi* (throughout the breeding range from Anacapa Island, California, to San Benito Islands, Baja California), with little or no white in front of or above the eye (Figs. 2 & 3). The recognition of two subspecies (sometimes called the "Guadalupe" Murrelet and "Scripps" Murrelet) immediately raised concern for the viability of the nominate subspecies, which appeared to be limited to Guadalupe Island. Feral cats apparently had extirpated murrelets on the main island of Guadalupe, and *S. h. hypoleucus* murrelets seemed restricted to cat-free offshore islets, a tiny fraction of former nesting habitats (Green & Arnold 1939).

Since 1939, the nominate subspecies has been found to occur and breed regularly in small numbers at San Benito Islands (Jehl & Bond 1975, Whitworth *et al.* 2003b, Keitt 2005, Wolf *et al.* 2005). Jehl & Bond (1975) suspected that *S. h. hypoleucus* birds may have moved fairly recently from Guadalupe Island to the San Benito Islands, in response to overcrowding on Guadalupe nesting islets. Two nests of the nominate race were found at the same site in 1977 and 1978 on Santa Barbara Island, California, but one member of the pair was of intermediate plumage (Winnett *et al.* 1979). All other breeders examined in the same colony have been referred to *S. h. scrippsi*. Small numbers of the nominate subspecies were captured near colonies in southern California in 1976 and 1994–1997 (Winnett *et al.* 1979; HRC & D.L. Whitworth, unpubl. data), and at least one *S. h. scrippsi* murrelet has been recorded at Guadalupe Island (Jehl & Bond 1975). The occurrence of small numbers of individuals in intermediate plumage at the San Benito Islands indicates limited interbreeding between subspecies (Jehl & Bond 1975, Whitworth *et al.* 2003b, Keitt 2005, Wolf *et al.* 2005).

CONFUSION WITH CRAVERI'S MURRELETS

From April to October, Craveri's Murrelets co-occur with Xantus's Murrelets off the west coast of Baja California and in southern and central California (Brewster 1902, Grinnell & Miller 1944, Jehl & Bond 1975, Howell & Webb 1995). These species are similar in appearance, and caution must be exercised in analyzing at-sea count data (Karnovsky *et al.* 2005).

Whether Xantus's and Craveri's murrelets were distinct species, subspecies, or age variants was debated for some time (Anthony 1900, Grinnell 1915, Bent 1946; see summaries in Brewster 1902, Jehl & Bond 1975). Brewster (1902) carefully described each species, and Van Rossem (1915, 1926) further distinguished their plumages: wing linings (i.e. white in Xantus's versus mottled in Craveri's), base of the inner vanes of the distal primaries (i.e. white in Xantus's versus dusky in Craveri's), dark collar (present in Craveri's only), and dorsal coloration (i.e. browner in Craveri's, Figs. 3 & 4). Discussion of possible interbreeding continued (Van Rossem 1939, Jehl & Bond 1975). Blake (1972) listed Craveri's Murrelet as a subspecies of the Xantus's Murrelet. Recent phylogenetic analyses have laid the question to rest as genetic differences clearly warrant species designation (Friesen *et al.* 1996).

The breeding ranges of Xantus's and Craveri's murrelets do not appear to overlap, despite suggestions to the contrary for the San Benito Islands and Natividad Island. Although the type specimen of Craveri's Murrelet was obtained by Italian Frederico Craveri reportedly at Natividad Island in 1857, some later sources concluded that it was actually collected at Raza Island in the Gulf of California in 1856 (Cooke 1916, AOU 1957; but see Jehl & Bond 1975, Violani & Boano 1990). Craveri's Murrelet eggs were first collected at Raza Island in 1875 (Streets 1877). Several Craveri's Murrelets have been recorded at sea near the San Benito Islands in spring, when some post-breeding birds from Gulf of California colonies disperse up the west coast of Baja California to California (Jehl & Bond 1975, DeWeese & Anderson 1976). A relatively

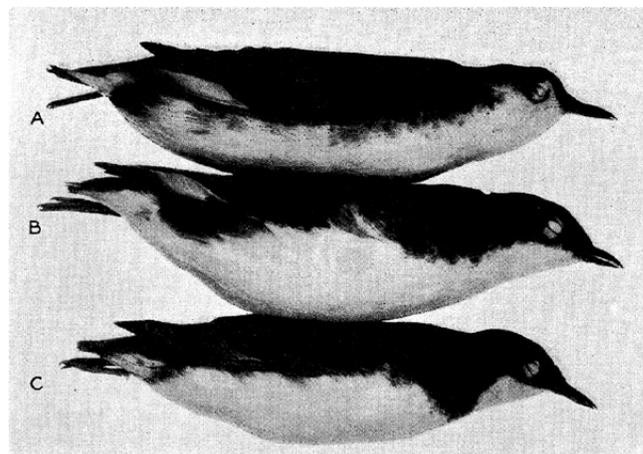


Fig. 3. "Specimens of the three murrelets, selected to show characteristic plumage differences: A. *Endomychura hypoleuca hypoleuca*, no. 17668, S.D.S.N.H. [San Diego Society of Natural History]; B. *Endomychura hypoleuca scrippsi* (type), no. 17934, S.D.S.N.H.; C. *Endomychura craveri* (showing maximum extension of dark collar), no. 15154, S.D.S.N.H." (Figure and caption reproduced with permission from Green & Arnold 1939: Fig. 16, copyright Cooper Ornithological Society)

large distance barrier (*c.* 1000 km) exists between breeding areas of the two species. Few islands with suitable nesting habitat occur between Asunción Island and Espíritu Santo Island (Brewster 1902, DeWeese & Anderson 1976). At Magdalena Island and Santa Margarita Island, murrelet breeding has not been documented, and several endemic mammals may prevent its occurrence (Nelson 1922). Craveri's Murrelets on the west coast of Baja California in spring most likely are subadults that have not returned to colonies in the Gulf of California. Surveys in February 2002 did not detect the presence of Craveri's Murrelets during the early breeding season at the San Benito Islands (Whitworth *et al.* 2003b, Keitt 2005), and no Craveri's Murrelet nests have been found outside of the Gulf of California (DeWeese & Anderson 1976).

DISCOVERY OF BREEDING COLONIES

To review discovery of the breeding distribution, we identified as "colonies" 13 geographically separated islands or groups of islands with breeding murrelets. We use the primary island for the colony name (except for San Roque/Asunción Islands which we considered within the same island group), and we take as first evidence of breeding the first reported nest site, backed up by museum egg records, published accounts, or unpublished reports. Breeding was first discovered by J.G. Cooper on Santa Barbara Island, California, in 1863 (Cooper 1868). Three more colonies were discovered 29–33 years later in Baja California by A.W. Anthony: Guadalupe Island (Walrus Bay, 1892, USNM #B25236), Coronado Islands (1893, USNM #B26319; Anthony 1899, 1900; Whitworth *et al.* 2003c), and San Benito Islands (1896; Whitworth *et al.* 2003b; WFWZ #11804). Colonies continued to be discovered in the twentieth century: Anacapa Island in 1911 (H.C. Burt; WFWZ #80,896 and #80,897; Willett 1912; Peyton 1913; McChesney *et al.* 2000), Santa Cruz Island in 1928 (M.C. Badger; WFWZ #92,441), San Jerónimo (also spelled "San Geronimo") Island in 1932 (N.K. Carpenter; USNM #B46624), Todos Santos Islands in 1940 (E.E. Sechrist; WFWZ #145,114), Santa Catalina Island in 1967 (Hunt *et al.* 1979), San Miguel Island in 1968 (Crossin & Brownell 1968, Huber 1968), San Clemente Island in 1976 (Hunt *et al.* 1979), and San Roque/Asunción Islands in 1977 (Drost & Lewis 1995; see Bancroft 1927). Nesting on San Martín Island has been long suspected, but a nest has yet to be found (Kaeding 1905, Keitt 2005).

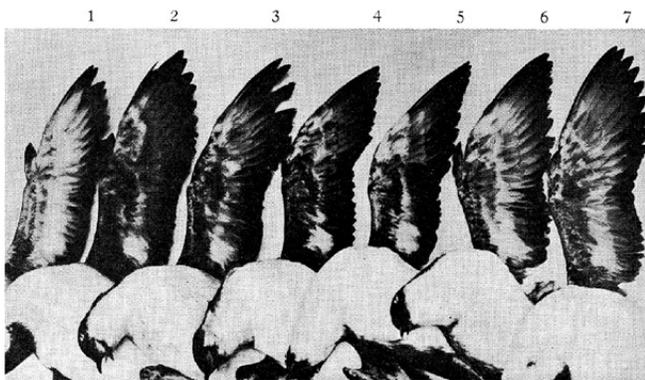


Fig. 4. "Specimens of *Brachyramphus hypoleucus* (No. 1) and *B. craveri* (Nos. 2–7), showing color of wing linings". (Figure and caption reproduced with permission from van Rossem 1915: Fig. 26, copyright Cooper Ornithological Society)

San Miguel Island (*c.* 34°N) and Asunción Island (*c.* 27°N) are the northernmost and southernmost breeding islands, respectively. Nesting areas are relatively accessible to researchers on foot only on certain portions of Santa Barbara, Coronado and San Benito Islands (Murray *et al.* 1983; Drost & Lewis 1995; Whitworth *et al.* 2003b, 2003c; Wolf *et al.* 2005). Nesting under shrubs has been described on Santa Barbara Island, Afuera Islet (off Guadalupe Island) and occasionally on the Coronado Islands (Murray *et al.* 1983, Carter *et al.* 1992, Whitworth *et al.* 2003c, Keitt 2005), while nesting in sea caves occurs on Anacapa, Santa Cruz and Coronado Islands (Whitworth *et al.* 2005; HRC, unpubl. data). Xantus's Murrelets also use sheer cliffs and very steep slopes for nesting at several Channel Islands breeding colonies (Hamer *et al.* 2003, 2005; HRC, unpubl. data), which suggests a much wider distribution on larger islands than is known from discovered nests alone.

DISCOVERY OF NORTHERN AT-SEA RANGE

Xantus's Murrelets were not reported in central California at Monterey Bay (*c.* 36°N) until 1894 (Brewster 1902). By 1925, many specimens had been collected between Monterey Bay and the Mexican border (Beck 1910; Van Rossem 1915, 1926). In 1910, murrelets were recorded farther north off Tomales Bay, Marin County, California (*c.* 38°N; Dawson 1923) and in April 1926 off Point Arena, Mendocino County, California (*c.* 39°N; Grinnell & Miller 1944). The first record north of California was that of two birds collected and others seen about 200 km SSW of Cape Flattery, Washington (*c.* 47°N), on 7 August 1947 (Cowan & Martin 1954; UBCZM #1518 and #1519). Jehl & Bond (1975) referred those specimens to the nominate subspecies. Subsequently, Feinstein (1958) reported an earlier beached specimen of *S. h. scrippsi* at Copalis Beach, Washington on 6 December 1941. The first Oregon record occurred far offshore in November 1969 (Scott *et al.* 1971).

The northern limit of the at-sea range of Xantus's Murrelets apparently occurs in British Columbia at about 52°N (Drost & Lewis 1995; Karnovsky *et al.* 2005; K.H. Morgan, unpubl. data). The first sight record (*S. h. scrippsi*, based on a drawing) in British Columbia was obtained on 14 July 1948 about 29–32 km west of the Goose Islands (*c.* 52°N) by C.J. Guignet (unpubl. field notes). The first specimens obtained in British Columbia were collected in October and November 1971 between Vancouver Island and the Queen Charlotte Islands (Sanger 1973). One specimen (UWBM #26813; 25 October) is referable to *S. h. scrippsi* (see photograph with incorrect specimen number in Campbell *et al.* 1990) whereas the other (UWBM #16809, 16 November) could not be assigned to subspecies because only a partial skeleton was preserved. At-sea surveys in the 1970s and 1990s demonstrated that substantial numbers of both subspecies regularly move into waters as far north as central British Columbia in late summer and fall (Wahl 1975; Karnovsky *et al.* 2005; K.H. Morgan, unpubl. data). In fall 2001, at least 90% of 106 Xantus's Murrelets seen more than 90 km from shore off Oregon and Washington were referred to the nominate subspecies (Mlodinow *et al.* 2002).

SOUTHERN LIMIT OF AT-SEA RANGE

During the non-breeding season, Xantus's Murrelets are rarely found south of the southernmost breeding colony at Asunción Island (*c.* 27°N), but have been noted to just south of Magdalena Bay (*c.* 24°N; Brewster 1902, Anthony 1925, Jehl & Bond 1975, Howell & Webb 1995, Karnovsky *et al.* 2005). The two *S. h. hypoleucus*

specimens collected by Xantus near Cabo San Lucas in 1859 and 1860 remain the southernmost records (*c.* 23°N). Similarly, the southernmost record of Ancient Murrelets is from Punta Arena near Cabo San Lucas in December 1995, and the three individuals involved are considered vagrants, because the next closest record is from 1700 km north, near the US–Mexico border (Sealy & Carter 2004). Craveri's Murrelet holds the distinction of being the most southerly breeding (*c.* 24.5°N) and wintering (*c.* 21°N) alcid (DeWeese & Anderson 1976, Howell & Webb 1995, Gaston & Jones 1998).

CONSERVATION

Concern about the status of Xantus's Murrelet developed in the 1990s based on

- its relatively small world population size and restricted breeding range (Drost & Lewis 1995, Gaston & Jones 1998);
- poor breeding success, high predation and declining population size at the largest US colony (Santa Barbara Island, California);
- introduction of mammalian predators at most breeding islands (McChesney & Tershy 1998); and
- threats at sea, especially oil (Murray *et al.* 1983; Carter *et al.* 2000).

Since the mid-1990s, introduced predators have been removed from several nesting islands (see Hamer *et al.* 2005, Keitt 2005, Whitworth *et al.* 2005), and new studies of breeding biology (Roth *et al.* 2005, Whitworth *et al.* 2005, Wolf *et al.* 2005), physiologic health (Newman *et al.* 2005) and population status (Whitworth *et al.* 2003a, 2003b, 2003c, 2005; Keitt 2005; HRC, unpubl. data) have been conducted. In 2004, Xantus's Murrelet was listed as Threatened under the *California Endangered Species Act* (Burkett *et al.* 2003), and a decision is pending whether to list the species under the *US Endangered Species Act*. It is listed as Threatened in Mexico (Keitt 2005) and is not currently listed in Canada.

SYMPOSIUM

Despite the relatively high level of research and conservation action since 1990, little peer-reviewed literature has been produced. A special symposium, "Biology and Conservation of the Xantus's Murrelet," was held at the joint meeting of the Pacific Seabird Group and Waterbird Society in Portland, Oregon, on 20 January 2005. The aims of the symposium were to increase awareness in scientific, agency and conservation communities concerning the plight of Xantus's Murrelet and to promote publication of recent findings, both in this issue of *Marine Ornithology* and in another symposium issue (in preparation) of the *Proceedings of the Western Foundation of Vertebrate Zoology*. Symposium papers have greatly augmented available information on this little-known species.

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AT-SEA DISTRIBUTION, ABUNDANCE AND HABITAT AFFINITIES OF XANTUS'S MURRELETS

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SUMMARY

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We used shipboard and aerial surveys at sea to study distribution, abundance and habitat affinities of Xantus's Murrelets *Synthliboramphus hypoleucus* within their range, including waters from British Columbia to southern Baja California, and to 500 km offshore. We recorded 1628 murrelets during strip-transects conducted in most years from 1975 to 2003. Densities were highest over the continental slope (depths 200–1000 m) at distances 25–150 km offshore. Murrelets were most numerous in warmer waters of lower salinity, a pattern consistent each year regardless of El Niño–Southern Oscillation or Pacific Decadal Oscillation anomaly fluctuations. During the breeding season, murrelets concentrated in the Southern California Bight (SCB), with lower densities off Baja California and from Point Conception to Bodega Bay, California. During the nonbreeding period, they dispersed north as far as northern Vancouver Island, British Columbia, although densities were highest from central Baja California to central Oregon. We used generalized additive models to estimate the abundance of this species at sea. We observed no trends in abundances across years, 1975–2001 (SCB), and 1985–2003 (central California). After adjustment for biases in survey data, our estimate for the total number of Xantus's Murrelets in North America during the nonbreeding season (1975–2003) is 39 700 birds, consisting of an estimated 17 900 breeding birds (95% confidence interval = 13 900 to 21 000) and 21 800 subadults/nonbreeders.

Key words: At-sea behavior, distribution, ocean habitat, population size, *Synthliboramphus hypoleucus*, Xantus's Murrelet

INTRODUCTION

Xantus's Murrelet *Synthliboramphus hypoleucus* is endemic to the Pacific coast of North America, ranging at sea from 52°N off British Columbia to 23°N off Baja California, Mexico, and to about 500 km offshore (Drost & Lewis 1995, Carter *et al.* 2005). Waters frequented by this murrelet encompass *c.* 1 665 000 km². The global population is divided into two subspecies: *S. h. hypoleucus* (hereafter *hypoleucus*), which breeds almost entirely on Guadalupe Island (with some at the San Benito Islands) off central western Baja California, Mexico; and *S. h. scrippsi* (hereafter *scrippsi*) which breeds primarily on the Channel Islands and Coronado Islands within the Southern California Bight (SCB), but also as far south as the San Benito Islands where it overlaps with *hypoleucus* (Jehl & Bond 1975, Carter *et al.* 2005, Keitt 2005, Wolf *et al.*

2005; Fig. 1). The pelagic distributions of both subspecies overlap to a great extent during post-breeding dispersal in late summer and autumn, when both move primarily northward (Whitworth *et al.* 2000). In addition, Craveri's Murrelet (*S. craveri*, hereafter *craveri*), difficult to distinguish from Xantus's Murrelet in the field and an endemic breeder in the Gulf of California, Mexico, also disperses northward and co-occurs with Xantus's Murrelets along the coasts of Baja California and California during the nonbreeding season (Howell & Webb 1995, Carter *et al.* 2005).

In December 2004, the California Fish and Game Commission listed Xantus's Murrelet as a State Threatened species. It is among the least numerous of alcids and has been adversely affected from predation by rats *Rattus* sp., cats *Felis catus*, Deer Mice *Peromyscus maniculatus* and Barn Owls *Tyto alba* at islands where it nests

(Murray *et al.* 1983, Drost & Lewis 1995, McChesney & Tershy 1998, Keitt 2005). However, because of difficulties in censusing murrelets at their colonies, population estimates and trends for this species are only roughly known. Estimates of the breeding population at the primary Channel Islands colony (on Santa Barbara Island) during 1975–1977 ranged from 1500 to 10000 birds (Hunt *et al.* 1979, 1980; Sowls *et al.* 1980; Murray *et al.* 1983), although estimates during 1991–2002 (with allowance for censusing difficulties) indicated that the global breeding population was 10000 to 20000 birds (Drost & Lewis 1995; Carter *et al.* 1992, 2000; Keitt 2005). Springer *et al.* (1993) estimated the global population to be 16000 to 30000 birds, but that estimate used historical 1970s estimates for the Channel Islands.

Xantus's Murrelets nest in crevices and under bushes on steep rocky slopes, cliffs and boulder talus. Many nesting areas are not accessible. Estimates of colony size have been derived from

- nest-site counts in accessible areas,
- at-sea counts near colonies,
- extrapolations using available breeding habitat,
- at-sea nocturnal vocalization surveys, and
- at-sea nocturnal spotlight transects (summarized in Burkett *et al.* 2003).



Fig. 1. Breeding range of Xantus's Murrelets. Islands where murrelets breed are shown in italics (from Whitworth *et al.* 2003b).

None of these methods have been validated, and estimates lack confidence intervals. Yet, a measurement of estimated precision (reliability) is of considerable importance for effective management and conservation.

Because of these difficulties censusing colonies, Xantus's Murrelet is a good candidate for the use of an alternative method of estimating population size—at-sea surveys during the nonbreeding season. Use of at-sea surveys to estimate population size of seabirds has received much attention recently (reviewed in Clarke *et al.* 2003). The primary concerns have been development of standardized at-sea survey protocols (reviewed in Tasker *et al.* 1984), reduction in biasing factors (e.g. Spear *et al.* 1992, 2005), and development of a statistical method that can deal with biases hampering analyses of at-sea survey data and that provides reasonable 95% confidence intervals for such estimates (Clarke *et al.* 2003).

These primary biases are encountered during at-sea surveys:

- Bird movement relative to that of the ship (“flux”)
- Varying survey platforms (e.g. boat vs. plane)
- Varying survey methods (strip vs. snapshot)
- Variation in observer ability (see “Methods”)

Primary problems encountered when analyzing survey data (aerial and shipboard) have been the use of sample-based procedures on data that are often collected using a nonrandom survey design, and the patchiness of seabird distributions at sea. The former condition results in estimate inaccuracies (for example, if areas of high seabird density are surveyed in greater proportion than are areas having a lower density, abundance is overestimated), and the latter leads to lack of precision (high variances) and unwieldy confidence intervals, rendering the estimates themselves of little use.

The development of generalized additive models (GAMs; Hastie & Tibshirani 1990) and their subsequent use to estimate seabird population size and trend from at-sea surveys, has alleviated both of these concerns (Clarke *et al.* 2003). Unlike inference from sample-based methods, inference from model-based methods is not dependent on a random survey design. In addition, as compared with stratified methods, GAMs provide substantial improvements in precision (e.g. Borchers *et al.* 1997, Augustin *et al.* 1998), because GAMs capture nonlinear trends in density while using only a few parameters. GAMs also provide a method for smoothing time series of abundance estimates to estimate underlying trends (e.g. Buckland *et al.* 1992). Relevant to these advances, it is fortunate that the Xantus's Murrelet has been intensively surveyed by seabird biologists within its entire range during the past three decades.

For this paper, our objectives were

- to assemble as much available at-sea survey data as possible to provide good coverage of all parts of the range of Xantus's Murrelets during the breeding and nonbreeding periods.
- to describe the birds' oceanographic habitat affinities.
- to estimate the abundance of the species within its at-sea range during the breeding and nonbreeding seasons.
- to compare estimated pelagic population size in the SCB averaged over the breeding seasons of 1975–1978 versus population size averaged for the 1999–2001 period.

- to estimate the annual trend in population size of murrelets occurring off central California during the breeding season using survey data collected each year from 1985 to 2003.

We amassed data from 11 at-sea studies that, together, provided thorough coverage throughout the pelagic range of this species. The total area surveyed was 65 180 km² of ocean, or about 9% of the total pelagic range of Xantus's Murrelets. This amount of survey coverage of a population's pelagic range is more than adequate for the purpose of providing an accurate estimate of population size when using GAMs (Clarke *et al.* 2003, Spear *et al.* 2003).

METHODS

Study area

We conducted surveys in waters from 16.8°N to 54.5°N, from the coast to well beyond 600 km offshore. However, we recorded no Xantus's Murrelets north of 52.46°N (132.71°W), south of 24.14°N (113.18°W), or beyond 555 km offshore. We therefore confined our analyses to surveys conducted from 23°N to 53°N, and to about 600 km offshore (Fig. 2). This species' range is not known to extend beyond those latitudes or distance offshore.

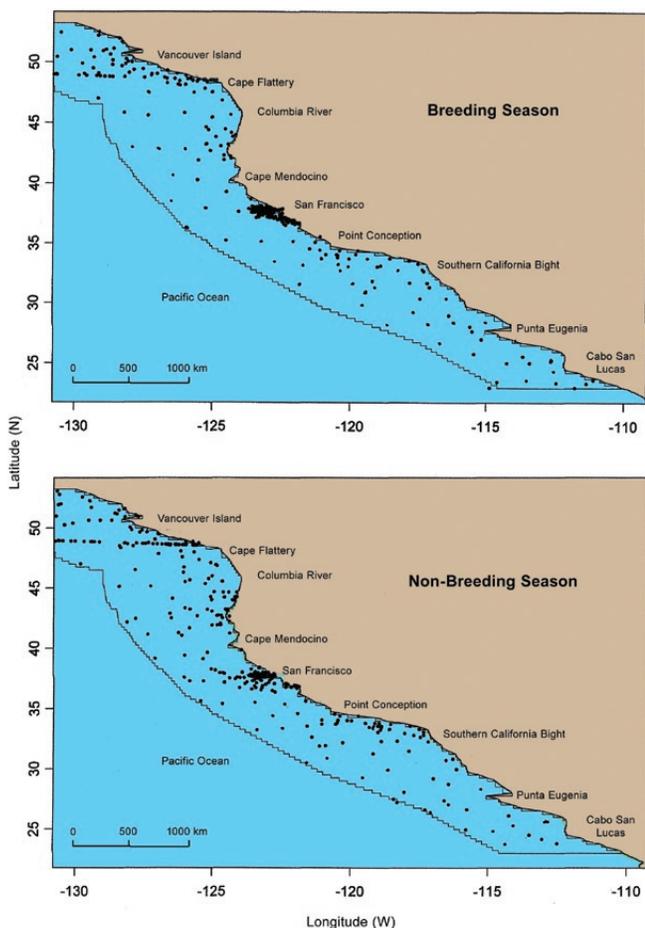


Fig. 2. Study area and survey effort for breeding season and nonbreeding season surveys off the Pacific coast of North America (53°N to 23°N). Each dot represents one noonday position. Many positions were repeatedly sampled in different years; see “Methods” for number of survey transects.

Factors biasing survey data

Primary biases potentially problematic in this study are these:

- 1) Effects of bird movement relative to that of the ship
- 2) Varying survey platforms
- 3) Variation in observer ability
- 4) Undercounting birds that dive ahead of the ship or plane, especially when ship or plane surveys were conducted using only one observer on watch
- 5) Overcounting because of inclusion of *craveri* in counts of *hypoleucus/scrippsi*

We avoided the first bias by using the “vector” method (Spear *et al.* 1992) during central California, GLOBEC (global ocean ecosystems dynamics), and EPOCS (Eastern Pacific Ocean Climate Study) studies (41% of total survey effort; Table 1) and by applying the correction factor found in those studies to data from studies for which the vector method could not be used (details below). The vector method has been validated with favorable results (Clarke *et al.* 2003). Although two survey platform types were used (boat and plane), the second bias was not a problem because similar abundance estimates are obtained by each (Briggs *et al.* 1985).

The best way to reduce the third and fourth biases is to use multiple observer teams (Verner 1985). Indeed, apart from reducing the effect of observer differences, the use of multiple observers on watch simultaneously is required to detect 95% of the birds in a survey quadrant. This is true especially for smaller species such as murrelets for which a single observer detects, on average, 26% fewer birds than two observers on watch together (Spear *et al.* 2005). Bias from undercounting diving birds can also be reduced by use of multiple observer teams. Multiple observer teams were used in central California, GLOBEC, and EPOCS studies, but single observers were used in other studies. An exception was aerial surveys in which two observers were often on watch simultaneously. However, each aerial observer scanned a different strip, one on each side of the plane. See “Discussion” for qualifications regarding negative bias caused by diving birds and use of single observers, and positive bias caused by inclusion of *craveri* in count data.

Survey protocol

All surveys were conducted as strip surveys. During studies conducted from ships (Table 1), we conducted continuous strip-surveys from the flying bridge while the ship was underway. Xantus's Murrelets seen within a 90-degree quadrant of known width (300–600 m wide depending on height of the ship's flying bridge) off one forequarter were counted. An exception was the Canadian Wildlife Service (CWS) surveys, most of which were used a 300-m strip width, but with two 150-m strips surveyed simultaneously, one off each of the boat's quarters centered on the bow. For aerial surveys (MMS [Minerals Management Service] II, MMS III, and USGS/HSU [US Geological Survey/Humboldt State University]), all birds were counted within 50-m strips on one or both sides of the aircraft (one observer per side) flying at a 60-m elevation (Briggs *et al.* 1987, Mason *et al.* 2004). By noting ship or plane speed, we calculated surface area of ocean surveyed.

Information recorded for each sighting during the GLOBEC, SFDODS (San Francisco Deep Ocean Disposal Site), EPOCS, Rockfish I, and Rockfish II studies (Table 1) were number of birds and behavior (sitting on water or flying in transit). During those

surveys we also recorded flight direction to the nearest 10 degrees. For all other studies, we did not record flight direction; only number of birds and behavior were recorded.

For nearshore shipboard surveys (GLOBEC, SFDODS, Rockfish I, Rockfish II, SWFSC [Southwest Fisheries Science Center], CWS; Table 1) survey effort was divided into 15-minute "transect" periods, with ship speed at about 18 km/h. For the offshore EPOCS study (where environmental variables changed over a larger spatial scale), survey effort was binned into 30-minute transects with ship speed at about 28 km/h. Aerial surveys, including inshore and offshore regions, were flown at about 165 km/h, with survey effort binned into 5- to 6-minute transects. Data recorded at the beginning of each transect during all studies included date, position, ship or plane speed, and course. The average ocean area surveyed for 15-minute and 30-minute boat and aerial transects was $1.33 \pm 0.74 \text{ km}^2$ ($n = 35\,206$ transects; unless noted otherwise, this paper presents means ± 1 standard deviation [SD])— $6.53 \pm 1.80 \text{ km}^2$ ($n = 1015$) and $0.38 \text{ km}^2 \pm 0.14$ ($n = 30\,400$), respectively. Respective transect line lengths were 4.4, 13.1, and 4.7 km.

During GLOBEC, SFDODS, Rockfish I, Rockfish II, and EPOCS studies, we also recorded these variables for each transect:

- Sea-surface temperature (degrees Celsius) and salinity (ppt)
- Thermocline depth (m) and strength (degrees Celsius change at 20 m below thermocline; details below)
- Wind direction (nearest 10 degrees) and speed (km/h)
- Ocean depth (m)
- Distance to mainland (km)

Environmental data were not available for other studies listed in Table 1. Thermocline depth and strength (i.e. indices of mixing in the water column) were monitored using expendable bathythermographs (XBTs) or conductivity–temperature–depth profilers (CTDs), generally producing a temperature profile to at least 200 m below the ocean surface (except in shallower waters). Values of thermocline depth and strength were extrapolated for survey transects that occurred between XBTs or CTDs. Thermocline depth (in meters) is the point where the warm surface layer meets cooler water below, which we identified as the strongest of the shallower inflection points determined from data printouts in which temperature was plotted as a function of depth. Exceptions occurred where there was no inflection point, and in that case the thermocline was considered to be at the ocean surface. Inflection points (warm to cold) near the surface were ignored because these reflect the warming of the ocean surface by the sun instead of mixing in the water column. We measured thermocline strength as the temperature difference (nearest 0.1°C) between the thermocline and a point 20 m below it. A region with strong upwelling or a strong front has a shallow, weak thermocline; the reverse is true where little mixing is occurring.

For survey data in which flight direction was recorded (see above), we used vector analysis (Spear *et al.* 1992) to adjust observed counts to correct for movement of flying birds relative to the ship (flight speeds as related to wind speed were taken from Spear & Ainley 1997). This adjustment is required when estimating abundance from shipboard surveys because the use of observed counts generally results in density overestimation, particularly for fast fliers such as murrelets. However, because of the high

TABLE 1
Summary of studies of at-sea seabird distribution along the Pacific coast of North America which contributed data on Xantus's Murrelets between 23°N and 53°N and within 560 km of the mainland

Study	Period	Years	Latitude	Area surveyed (km^2)	Murrelets (n)	Investigators
Southern California Bight (SCB)						
SCB I	75–78	4	32.5–34.0	5 371.8	293	Hunt/Ford
SCB II ^a	75–78	4	32.3–34.4	1 638.5	174	Briggs/Ford
USGS/HSU ^a	99–02	4	32.5–35.5	1 885.8	184	Carter/Mason
Central California						
Rockfish I	85–94	10	36.3–38.5	9 908.0	288	Ainley/Spear
SFDODS	95–02	7	36.8–38.0	4 586.3	96	Ainley/Spear
Rockfish II	97–03	7	37.0–38.1	4 025.8	22	Keiper/Ainley
British Columbia to Baja California						
MMS ^a	80–90	6	34.4–48.4	8 160.5	170	Briggs/Ford
EPOCS	79–95	12	26.5–48.5	6 629.6	32	Ainley/Spear
CWS	82–01	13	47.0–54.5	10 938.9	15	Morgan/Amey
SWFSC	88–01	8	16.8–48.0	10 380.2	344	Ballance/Pitman
GLOBEC	00–02	2	41.9–44.7	1 654.2	10	Tynan/Ainley
Total	75–03	77	16.8–54.5	65 179.6	1 628	

USGS = US Geological Survey; HSU = Humboldt State University; SFDODS = San Francisco Deep Ocean Disposal Site; MMS = Minerals Management Service; EPOCS = Eastern Pacific Ocean Climate Study; CWS = Canadian Wildlife Service; SWFSC = Southwest Fisheries Science Center; GLOBEC = global ocean ecosystems dynamics.

^a Study conducted aerially; all others were conducted shipboard.

proportion of observations of stationary murrelets (87%) in studies for which behavior was available, adjustment for movement in those data resulted in a reduction (correction for flux) of only 8.4% from recorded counts. We used that value to adjust counts of murrelets recorded in shipboard studies when flight direction was not recorded. However, we considered that adjusting murrelet counts for the effect of movement was unnecessary for aerial survey data because of the low proportion of murrelets recorded in flight, and because murrelet flight speed is much slower than survey aircraft, thus vastly reducing the effect of bird movement on count accuracy (Spear *et al.* 1992).

We used the data from GLOBEC, SFDODS, EPOCS, Rockfish I and Rockfish II studies to examine distribution of birds in relation to ocean depth and distance to land. We did not include SCB surveys in such analyses because those data may be confounded with colony attendance. That is, birds seen during daylight within 100 km of colonies may reflect a restricted foraging range related to nocturnal colony attendance during the breeding season (Whitworth *et al.* 2000).

Habitat affinities

To understand how murrelet density is related to habitat variables, we used Rockfish I and II and SFDODS data. These surveys were conducted throughout the year (5 January to 27 December). Habitat variables included sea-surface temperature and salinity, thermocline depth and strength, wind speed, ocean depth and distance to mainland. We also considered temporal effects by plotting densities relative to Julian dates and year. The sample unit in these analyses was one survey transect; average transect length was 4 km. Transect densities were weighted by surface area of ocean surveyed to control for differences in survey effort.

To examine murrelet densities off central California (1985–2003) in relation to El Niño Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO), we used ENSO and PDO anomaly indices from <ftp://ftp.prd.ncep.noaa.gov/pub/cpc/wd52dg/data/indices/ssstoi.indices> and <http://jisao.washington.edu/pdo/PDO> latest respectively. The ENSO index is the average sea-surface temperature (SST) anomaly equatorward of 5 degrees latitude (north and south) in the tropical Pacific (120°W to 170°W). Annual anomaly values are averaged monthly values for each year. The PDO index reflects standardized values derived as the leading principal component (PC) of monthly SST anomalies in the North Pacific, poleward of 20°N. Monthly mean global average SST anomalies are removed to separate this variability from any “global warming” signal in data. For this analysis we also calculated an annual murrelet density anomaly by subtracting murrelet density averaged across all years from murrelet density observed in each year.

Generalized additive models

GAMs were used to estimate population size from at-sea survey data. GAMs are an extension of generalized linear models (GLMs; McCullagh & Nelder 1989). One advantage of GLMs and GAMs over linear models is their ability to cope with errors that are not normally distributed. Linear models can be expressed as

$$E[y] = \beta_0 + \sum_k \beta_k x_k$$

where y is the response variable, $E[y]$ represents the expected value of y , x_k is the k th explanatory variable (covariate) and the β s are constants estimated from data. The right-hand side of the equation

is the linear predictor. GLMs allow the linear predictor to be a nonlinear function of expected observations,

$$g(E[y]) = \beta_0 + \sum_k \beta_k x_k$$

where $g(\cdot)$ is the link function defining the relationship between the response and the linear predictor. The principal strength of additive models is their ability to fit complex smooth functions in the predictor rather than being constrained by the linearity implicit in GLMs. A GAM is expressed as

$$g(E[y]) = \beta_0 + \sum_k S_k(x_k).$$

The right-hand side of the equation is the additive predictor. β_0 is an intercept term and S_k is a one-dimensional smoothing function for the k th spatial covariate, x_k . The degree of smoothing is determined by the degrees of freedom (df) associated with the smoothing function. Larger dfs have less smoothing with more flexible functions. A GAM in which all the smoothing functions have one df is equivalent to a GLM. An offset (a linear covariate whose coefficient is 1) can also be included in the predictor. This is useful when a transformation of the response variable can be modeled using a standard distribution. For example, rather than modeling density, we could model numbers, with area surveyed as an offset.

Modeling spatial distributions

GAMs were fitted using observed murrelet counts during each survey transect as the response variable. Transects outside study areas were excluded. Explanatory variables considered for each model were latitude, longitude, shortest distance to mainland, ocean depth and distance to breeding colony. Ocean depth and distance to mainland were calculated for each transect using transect position along with coastline and bathymetry data obtained respectively from <http://rimmer.ngdc.noaa.gov/coast/> and <http://ingrid.ldgo.columbia.edu/SOURCES/WORLDBATH>. The northernmost, primary colony on Santa Barbara Island (c. 33.45°N, 119.02°W; Fig. 1) was the designated colony location. GAMs are constrained to use a single colony position. The fact that other large Xantus's Murrelet colonies exist at the Coronado Islands and Guadalupe Island, with smaller ones at Santa Cruz, Anacapa, and San Benito Islands was not a problem because the density relationship with colony location was modeled as nonlinear. High densities in association with other distant colonies are readily modeled with GAMs even with multiple colony locations (see below).

Count data are often modeled using a Poisson error structure, with variance equal to the mean (McCullagh & Nelder 1989). However, when birds occur in clusters, variance of counts is more dispersed than is implied by a Poisson distribution. Therefore, we modeled those data using the Poisson variance function and estimating a dispersion parameter, which we incorporated into model selection procedures (e.g. Venables & Ripley 1997). Observed counts must be adjusted for bird movement, and they depend on area surveyed within the transect, so we used the logarithm of area surveyed multiplied by the bird-movement adjustment factor (which varies for each data point) as an offset. The logarithm was used because we used a log link function.

Model selection with GAMs involves choosing explanatory variables and their degree of smoothing. Forward stepwise selection was used to select covariates for each model on the basis of Akaike's (1973) information criterion. Each covariate was included as a linear term or smooth (curvilinear) term with 4 df. Residual plots

were examined to ensure that model fits were adequate. Because bird clusters could overlap adjacent survey transects, counts were not necessarily independent. Thus, current model-selection methods, which assume observations are independent, could result in overfitting. However overfitting should not bias the population size estimate, although its variance will increase (Augustin 1999), and the choice of a maximum of 4 df in the smooths reduced the possibility of overfitting.

Estimation of population size and temporal trend

Once fitted, a GAM provides a smooth average density surface over the area of interest, including unsampled areas. Population size was estimated by integrating numerically under this surface. First, we created a fine grid across the study area (grid cell size for each GAM given in figure captions for each distribution plot). The fitted surface was then used to predict the average number of birds in each grid square. Finally, population size was estimated as the sum of the predicted numbers over all grid squares within the study area.

Variance estimation

Confidence intervals for population size were obtained using bootstrapping. Bootstrapping involves creating many new data sets from the original sample, and analyzing these new samples in the same way as the original. The distribution of the statistic of interest is then estimated from its empirical distribution among the bootstrap samples.

To control for correlation between counts from survey transects close in space and time, we used an adaptation of a moving-blocks bootstrap (Efron & Tibshirani 1993). In this bootstrap technique, data are resampled with replacement from all possible contiguous blocks of some specified length. Block lengths are determined by accounting for strength of the autocorrelation between observations. The block must be long enough so that observations further than one block length apart are independent.

Because counts from survey transects within a day could be correlated, day was used as the sampling unit (block). The “length” of each day was measured as the number of transects surveyed. The resampling algorithm works through the data set, recreating each day’s data in turn. Generating data for a day involved randomly selecting a day from survey data and randomly selecting a transect to start from within that day. Counts for survey transects in the original day were then recreated in turn from survey transects in the new day using the semi-parametric bootstrap procedure (e.g. Davison & Hinkley 1997) described below. If the end of a day was reached before enough transects had been resampled, resampling was continued at the start of the next day. For data from the breeding season, there were an average of 22 transects per day. A bootstrap count b_i for transect i was generated from transect j , $b_i = \hat{f}_i + \hat{s}_i \varepsilon_j$ where $\hat{f}_i = E[y_i]$ is the fitted value for count i , \hat{s}_i is the estimated standard deviation for count i and ε_j is the deviance residual of count j . For overdispersed Poisson errors, \hat{s}_i is defined by $\hat{s}_i^2 = \hat{\phi} \hat{f}_i (1 - h_i)$ (Davison & Hinkley 1997), where h_i is the leverage of count i (McCullagh & Nelder 1989), and $\hat{\phi}$ is the estimate of the dispersion parameter ϕ .

A total of 199 bootstrap resamples were generated for each data set being modeled. The model was refitted to each bootstrap resample and a new population size estimate obtained. However, as is common with bootstrap resamples obtained from GAMs, these estimates were slightly biased. To adjust for this, they were rescaled by multiplying

by the ratio of the original estimate to the mean of bootstrap estimates. The coefficient of variation (CV) of the population size estimate was calculated by dividing the sample standard deviation of scaled bootstrap estimates by the original estimate of population size. Confidence intervals (95% CIs) were estimated using the percentile method (e.g. Davison & Hinkley 1997).

Population size estimates

Southern California Bight: 1975–1978 versus 1999–2002

To standardize survey protocols, we restricted analyses of the SCB to two studies conducted using aerial surveys between Point Conception and the US–Mexico border, and to data collected only during the central part of the colony attendance period (Fig. 3, 15 March–15 June; Murray *et al.* 1983, Drost & Lewis 1995, Whitworth *et al.* 2005a, Wolf *et al.* 2005). At that time, most breeding adults have returned from wintering areas (Whitworth *et al.* 2000), although some adults also may have dispersed back to wintering areas during this period because of high rates of nest failure (reviewed in “Discussion”). However, timing of breeding is about one month earlier in central Baja California than in the SCB

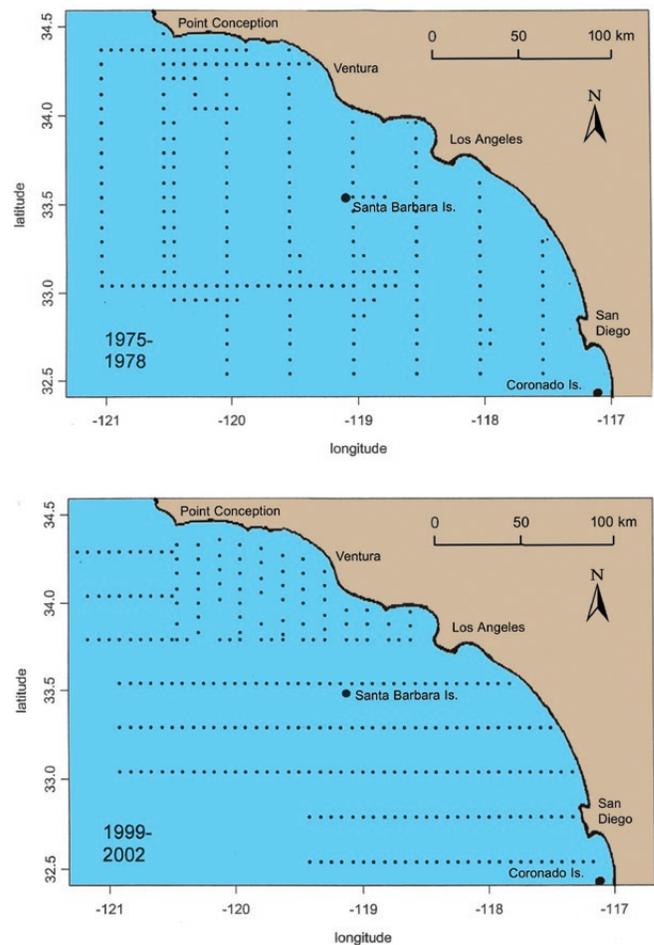


Fig. 3. Study area and survey effort for breeding season surveys in the Southern California Bight during MMS (*Minerals Management Service*) II aerial surveys (1975–1978; top) and USGS/HSU (US Geological Survey/Humboldt State University) surveys (1999–2001; bottom). Dots denote transect positions, many sampled repeatedly during different surveys and years; see “Methods” for number of survey transects.

(Wolf *et al.* 2005), such that some birds likely disperse northward from central Baja California colonies into the SCB before 15 June. After excluding data outside of the March–June period, and from north of Point Conception in 1999–2002, data for 1975–1978 (MMS II) included 336.7 km² (n = 756 survey transects) of survey effort, and that for 1999–2002 (USGS/HSU) included 502.4 km² (n = 837) of effort (Fig. 3). No surveys were conducted in the southern portion of the SCB within northern Baja California in either study.

Central California: 1985–2003

For consistency across years, we confined analyses of central California to data from surveys in waters within 80 km of Southeast

Farallon Island (SEFI). Because numbers of murrelets recorded in some years were too low to allow a GAM to perform adequately when analyzing each year separately, we grouped the data into three periods: 1985–1990, 1991–1997, and 1998–2003. To standardize data seasonally, we included only data collected during the breeding season from 15 March to 15 June. Survey effort for the breeding season within each period was 3278 km² (n = 2904 survey transects), 2380 km² (n = 1682), and 4114 km² (n = 3348).

Pacific coast of North America

We pooled data from 11 studies conducted from 1975 to 2003 within the pelagic range of Xantus's Murrelets (Table 1). We conducted two GAMs, one to estimate population size for the SCB breeding period (15 March to 15 June, see above), and the other for the remainder of the year, denoted here as the “nonbreeding” period. These periods accounted for major differences in distribution due to colony attendance during the breeding season. However, variation in timing of breeding between colonies and years likely resulted in some overlap between seasons (see “Discussion” for qualifications). Areas surveyed during breeding and nonbreeding periods were 21 844 km² (n = 23 604 survey transects) and 43 336 km² (n = 44 475 transects) respectively (Fig. 2).

RESULTS

Habitat affinities

In waters beyond foraging areas used by birds attending breeding colonies (see “Methods” for rationale regarding exclusion of waters within colony foraging range), the average ocean depth at which Xantus's Murrelets were recorded was 1528 m (SE = 55 m; n = 448 birds; range: 26–4589 m). Highest densities of Xantus's Murrelets were found over the upper continental slope (depth: 200–1000 m; Fig. 4[A]). Densities were moderately high over the outer slope (depth: 1001–3000 m), but were low over pelagic waters (depths > 3000 m), as well as over the continental shelf (depth < 200 m).

The average distance from the mainland at which murrelets were recorded was 83 km (SE = 2.5 km; n = 290 birds; range: 2–251 km). Densities of murrelets were highest at distances of

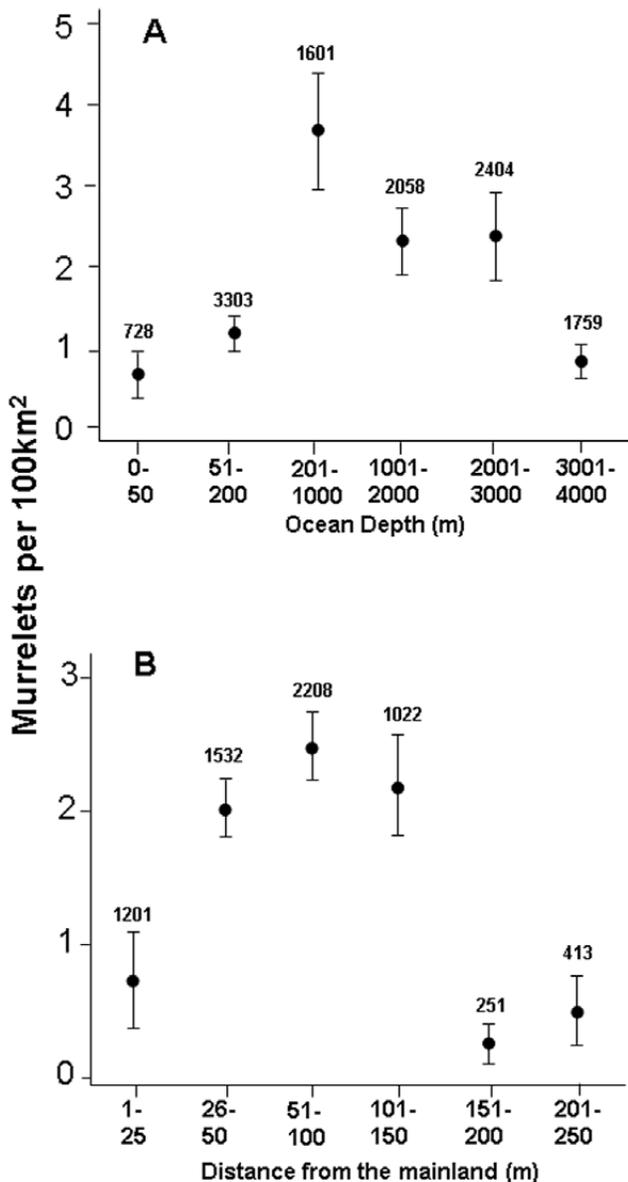


Fig. 4. Occurrence of Xantus's Murrelets (mean density \pm 1 standard error [SE]) in relation to ocean depth (A) and distance to the mainland (B). Only data for birds not associated with breeding colonies were analyzed. Sample sizes adjacent to means are numbers of transects.

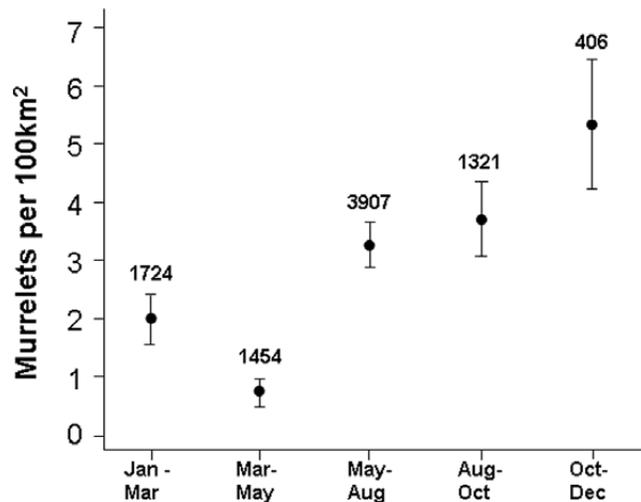


Fig. 5. Occurrence of Xantus's Murrelets (mean density \pm 1 standard error [SE]) in relation to time of year within waters off central California. Sample sizes adjacent to means are numbers of transects.

26–150 km from shore, but were low at distances < 26 km and > 150 km (Fig. 4[B]).

For the entire Pacific coast data set in the nonbreeding season, including SCB surveys, mean ocean depth was 1053 m (SE = 42 m; n = 810 sightings; group size: not distinguished), and mean distance to land was 70 km (SE = 2.7 km, n = 810 sightings). Our most distant records were sightings of seven birds more than 300 km from the mainland, including two birds at 42.15°N (302 km), one bird at 27.48°N (334 km), two birds at 47.25°N (432 km) and two birds at 27.72°N (555 km).

In central California waters, murrelet densities increased with Julian date (Fig. 5). Murrelet densities also increased with SST and thermocline strength; densities decreased with increases in sea-surface salinity and thermocline depth (Fig. 6). Thus, murrelet densities in that region were highest late in the year and were also

associated with high SST, low salinity, and a shallow but highly stratified thermocline. However, habitat variables were also highly correlated with each other and with Julian date. For example, Julian date was positively correlated with SST, salinity, thermocline strength and wind speed, and was negatively correlated with ocean depth, distance to land and thermocline depth (Table 2).

Relationship of ENSO and PDO to murrelet occurrence in central California

Although highest murrelet densities occurred during the warm-water ENSO years of 1992, 1997 and 1998 (Fig. 7), the relationship between density and the ENSO anomaly index was nonsignificant ($r = 0.176$, $n = 19$ years, $P = 0.5$). A similar relationship between density and the PDO anomaly index was also nonsignificant ($r = 0.201$, $n = 19$ years, $P = 0.4$, not shown; note that ENSO and PDO indices were highly correlated: $r = 0.553$, $n = 19$, $P < 0.02$). Interestingly, densities also were high during cool-water La Niña years (1989 and 2003).

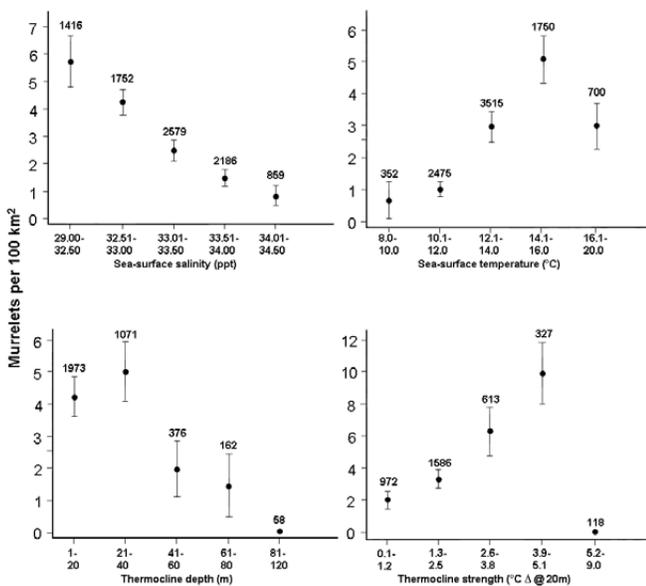


Fig. 6. Occurrence of Xantus's Murrelets (mean density ± 1 standard error [SE]) in relation to four oceanographic variables within waters of the Gulf of the Farallones. Sample sizes adjacent to means are numbers of transects.

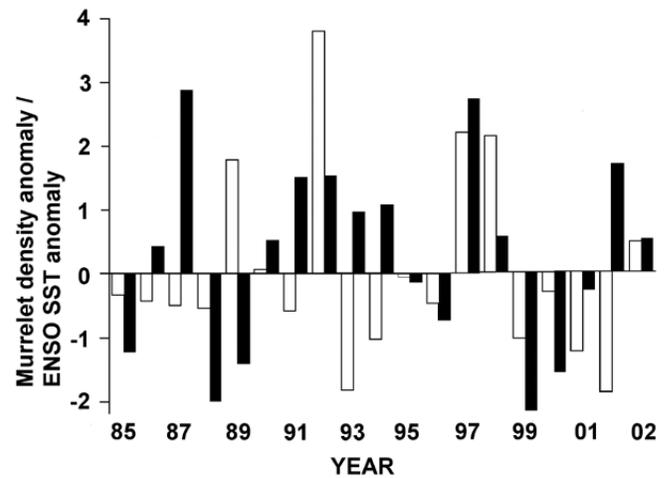


Fig. 7. Mean Xantus's Murrelet density anomaly (birds per 100 km²; white bars) and El Niño–Southern Oscillation (ENSO) sea-surface temperature anomaly (multiplied by 2; black bars) with respect to year. See “Methods” for details on calculation of anomaly values.

TABLE 2
Relationships (r values) between nine environmental and temporal habitat variables using Pearson correlation ($n = 3\ 616$ survey transects)

	SST	SAL	TDPT	TSTR	WSP	LAND	DEPTH	JD
SAL	-0.615 ^a							
TDPT	0.017	-0.181 ^a						
TSTR	0.407 ^a	-0.226 ^a	0.152 ^a					
WSP	-0.131 ^a	0.061 ^a	0.135 ^a	0.229 ^a				
LAND	0.176 ^a	-0.372 ^a	0.230 ^a	0.016	0.034			
DEPTH	0.279 ^a	-0.248 ^a	0.418 ^a	0.222 ^a	0.147 ^a	0.657 ^a		
JD	0.126 ^a	0.239 ^a	-0.305 ^a	0.362 ^a	0.267 ^a	-0.272 ^a	-0.027	
YEAR	0.496 ^a	-0.400 ^a	0.447 ^a	0.490 ^a	0.174 ^a	0.101 ^a	0.539 ^a	0.175 ^a

^a Significant correlation ($P < 0.05$).

SST = sea-surface temperature; SAL = sea-surface salinity; TDPT = thermocline depth; TSTR = thermocline strength; WSP = wind speed; LAND = distance to mainland; DEPTH = ocean depth; JD = Julian date.

Geographic distribution and population size estimates

CVs for the population size estimates indicated that GAMs generally performed well in modeling murrelet distributions at sea, particularly for the SCB during 1999–2001 and the entire population during the nonbreeding season (Table 3). Selected models included most or all covariates, although longitude was chosen least; distance to land and to Santa Barbara Island were chosen by each model (Table 4). Ocean depth and latitude were chosen in all models except in the GAM for the entire population during the breeding season.

Pacific coast of North America

During the breeding season, murrelets occurred from 44°N to 25.5°N, but were concentrated in the SCB (Fig. 8). During the nonbreeding season, they were more dispersed, occurring from southern Baja California to Vancouver Island, British Columbia, with the bulk between central Oregon and central Baja California. The area of

highest concentration during the nonbreeding season was off northern Baja California from about 28°N to 31°N (Fig. 8).

The CV of the population size estimate for the nonbreeding season was low (11.1%) and that for the breeding season was moderately high (19.3%; Table 3). The reason for the better fit of the former GAM was the more uniform distribution of murrelets over their pelagic range during the nonbreeding period, as compared with the highly clumped distribution in the vicinity of the SCB during the breeding period (Fig. 9). Population size estimates for breeding and nonbreeding seasons were about 24 500 and 36 100 birds, respectively (Table 3). As noted in the "Introduction," these estimates include *hypoleucus* and *scrippsi*, and a small proportion of *craveri* (see qualifications in "Discussion"). Using 95% CIs, no fewer than 16 600 birds and no more than 35 500 birds were present during the breeding season, and no fewer than 28 100 birds and no more than 43 700 birds were present during the nonbreeding season (Table 3).

Southern California Bight: 1975–1978 versus 1999–2001

The SCB distribution of murrelets during the breeding season differed between the 1975–1978 and 1999–2001 surveys (Fig. 9). During 1975–1978, there were two areas of high density: one near the California–Mexico border just to the northwest of the Coronado Islands, and the other in the vicinity of Santa Barbara Island. During 1999–2001, murrelets were present only in very low numbers in the southern area, and a more northern extension of the area of high density was seen in the Santa Barbara Island region.

Moderately low CVs for the two SCB population estimates (13%–15%) indicated that models were successful in fitting survey data (Table 3). Population size estimates for the number of murrelets occurring at sea in SCB waters during the breeding seasons of 1975–1978 and 1999–2001 were very similar at about 11 350 and 12 600 birds, respectively. Using 95% CIs, pelagic population sizes were not less than about 7500 birds and not more than about 14 200 birds in 1975–1978 and not less than 9150 birds and not more than 15 500 birds in 1999–2001.

Central California, 1985–2003

In central California, murrelets were concentrated over the mid-to-upper continental slope in all three periods (Fig. 10). However,

TABLE 3
Estimates of population size of Xantus's Murrelet for different areas, seasons and years, derived from generalized additive models (GAMs) using at-sea surveys, 1975–2003

Area	Birds (n)	95% CI	Coefficient of variation
Pacific coast of North America (23°N to 53°N), 1975–2003			
Breeding season	24 537	16 598–35 533	19.3
Nonbreeding season	36 098	28 103–43 699	11.1
Southern California Bight (32.5°N to 34.5°N), breeding season			
1975–1978 (aerial)	11 351	7 505–14 244	14.9
1999–2002 (aerial)	12 620	9 147–15 539	12.7
Central California (36.5°N to 38.5°N), breeding season			
1985–1990	261	128–367	22.9
1991–1997	517	331–702	17.9
1998–2003	293	182–366	17.5

CI = confidence interval.

TABLE 4
Covariates chosen by the generalized additive models when modeling distributions and estimating population sizes of Xantus's Murrelets

Population	Latitude	Longitude	Ocean depth	Distance to	
				Mainland	Colony
Pacific Coast of North America					
Breeding season	^a	Smooth	^a	Smooth	Smooth
Nonbreeding season	Smooth	^a	Smooth	Smooth	Smooth
Southern California Bight (breeding season)					
1975–1978	Smooth	^a	Smooth	Smooth	Smooth
1999–2001	Smooth	Smooth	Smooth	Linear	Smooth
Central California (breeding season)					
1985–1990	Smooth	^a	Smooth	Smooth	Smooth
1991–1996	Smooth	Smooth	Smooth	Smooth	Linear
1997–2003	Smooth	Smooth	Smooth	Smooth	Smooth

^a Covariate was nonsignificant in the model.

distribution in 1985–1990 was more uniform than in 1991–1996 or 1997–2003. During the 1991–1996 period, murrelets were more concentrated near Guide Seamount and Pioneer Canyon, and along the 1000-m depth contour. In the 1997–2003 period, they were found over the 500-m depth contour with two concentrations (50 km south of SEFI and over Cordell Bank).

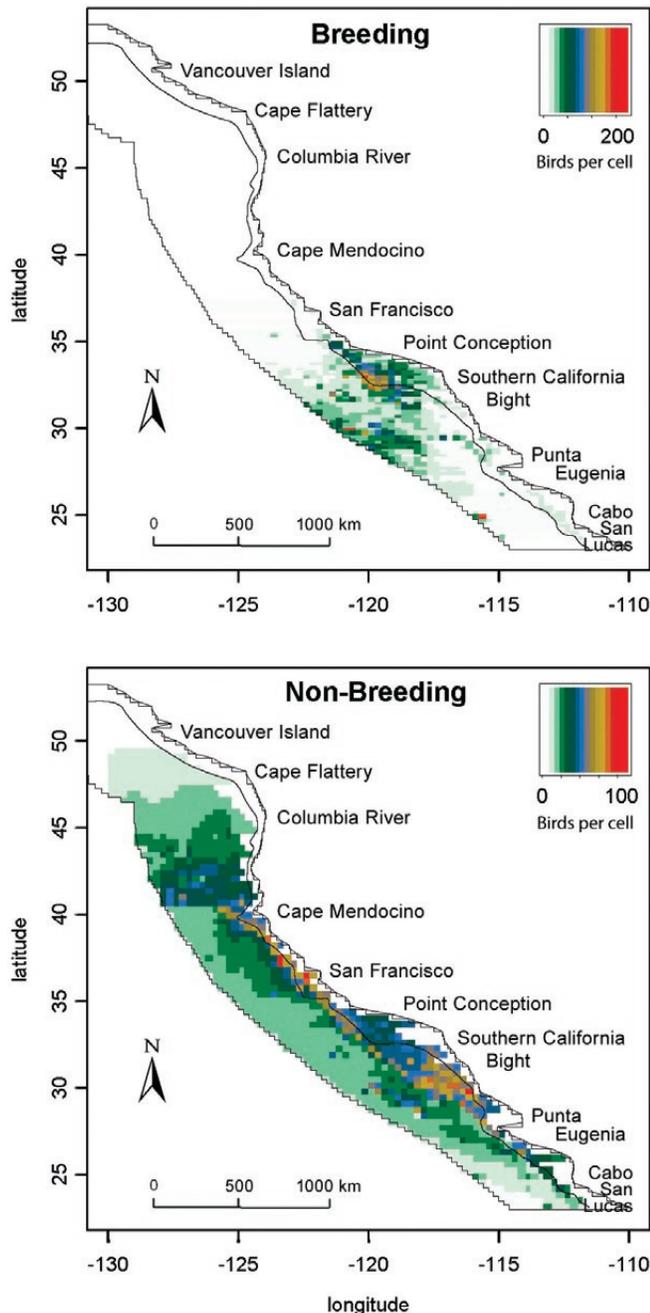


Fig. 8. Xantus's Murrelet distribution off the Pacific coast of North America (birds per 0.5×0.5 -degree cell) estimated from aerial and ship surveys during breeding and nonbreeding periods, 1975–2003. Number of birds per cell are smoothed values predicted and plotted using generalized additive models (GAMs). The total population estimate for each season is the sum of numbers across all blocks. Note that numerical scales represented by shading differ between the two periods. The dark line running offshore of the coast is the 200-m isobar, but the outer boundary is the limit of the study area.

CVs for population estimates of murrelet abundance during the three periods ranged from 17.5% to 22.9% (Table 3). Somewhat larger variances for the Central California estimates as compared with SCB estimates were attributable to the relative scarcity of these birds in the former location, resulting in a large proportion of zero densities per sample period.

Population size estimates (which represent the average for each year included within each of the three periods) ranged from 261 to 517 birds and did not show a significant linear trend ($P > 0.05$) across periods (Table 3). However, a curvilinear trend ($P < 0.05$) was observed because of higher numbers recorded mid-study. Using

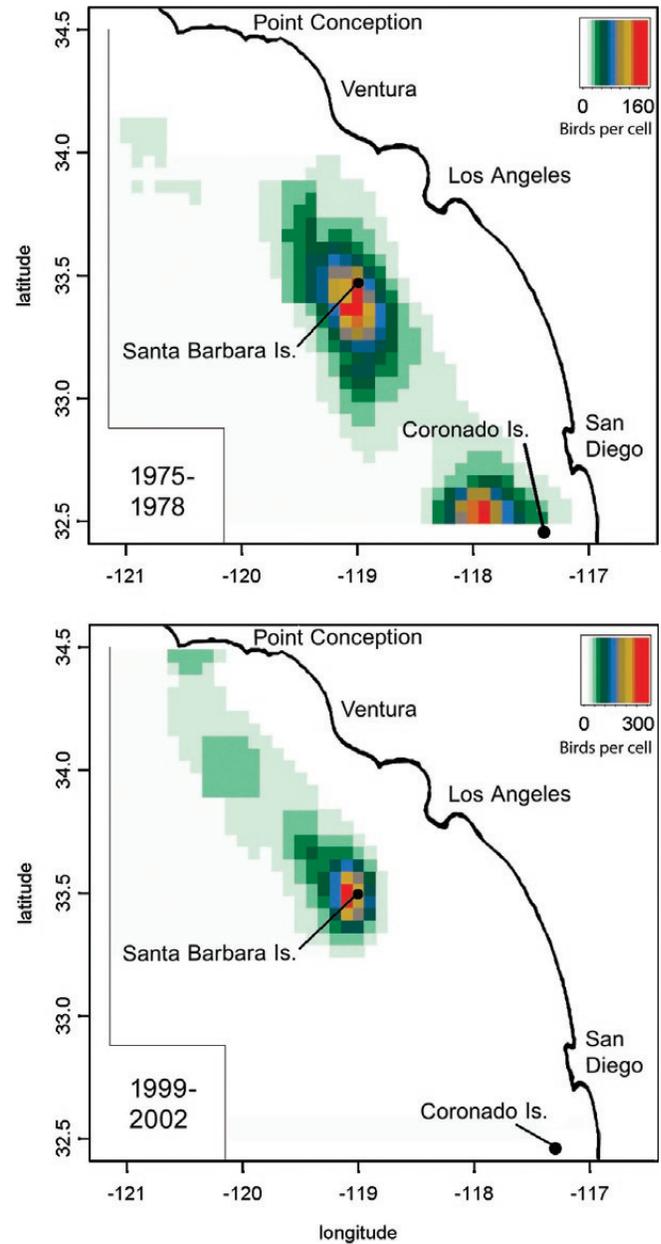


Fig. 9. Xantus's Murrelet distribution in the Southern California Bight (birds per 0.5×0.5 -degree cell) estimated from aerial surveys in 1975–1978 and 1999–2001. Estimates were output from generalized additive models (GAMs); shown as birds per grid block. See Fig. 8 for other format details.

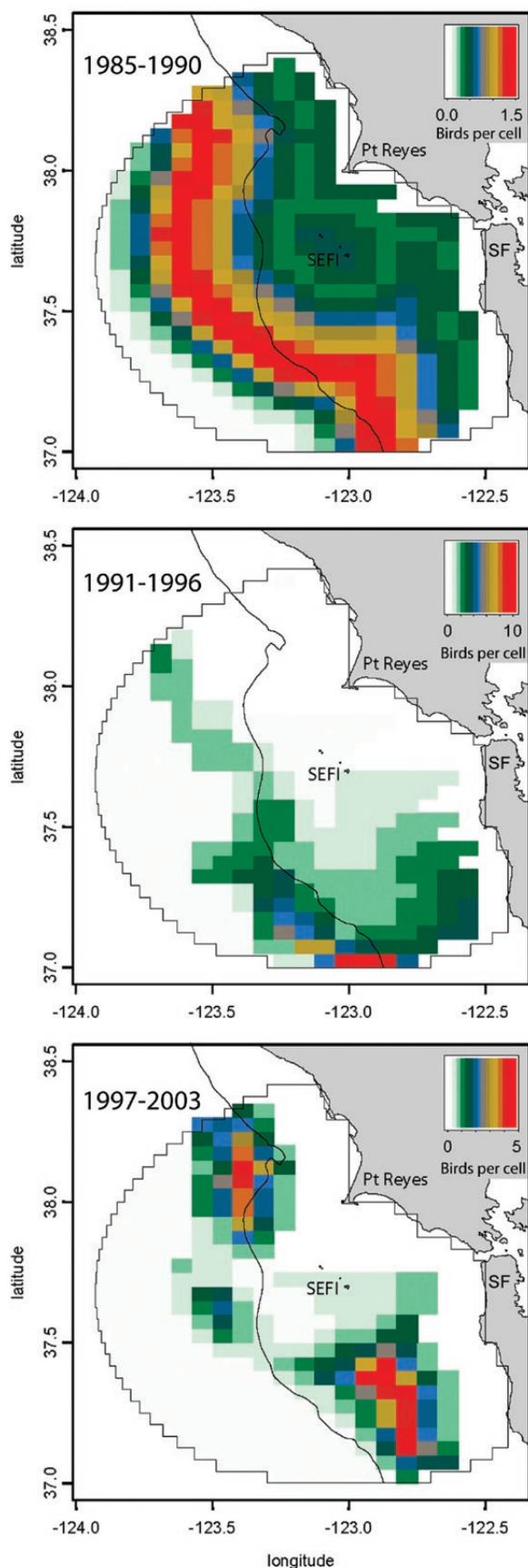


Fig. 10. Xantus's Murrelet distribution off central California (birds per 0.5×0.5 -degree cell) estimated from ship surveys in three periods between 1985 and 2003. See Figs. 8 and 9 for format details.

95% CIs, no fewer than 128–331 murrelets were present in the area during any given year (Table 3).

DISCUSSION

Although previous at-sea studies provided much information on at-sea occurrence and distribution of Xantus's Murrelets (Hunt *et al.* 1979, Briggs *et al.* 1987, Whitworth *et al.* 2000, Mason *et al.* 2004), this is the first study to provide a detailed analysis of these subjects for the entire pelagic range, plus habitat affinities and, in particular, an analysis of at-sea survey data to estimate global population size.

Survey caveats

As noted in "Methods," two factors that we could not account for during surveys could have negatively biased our count data:

- Birds that dive ahead of the approaching ship or plane before they are within the survey strip
- Use of single observers during 59% of our surveys.

Regarding the latter factor, Spear *et al.* (2005) found that a single observer detects about 26% fewer birds than two observers on watch simultaneously. A 20% deficit also was recorded for single (as compared with paired) observers conducting line transect surveys of Marbled Murrelets *Brachyramphus marmoratus* (Evans Mach *et al.* 2002). The potential effect of the former factor has not been quantified. However, in surveys to estimate population size of another alcid, the Common Murre *Uria aalge* (which dive for up to 112 s [Piatt & Nettleship 1985], much longer than averages of 18–24 s for Xantus's Murrelet [Hamilton *et al.* 2005]), this problem was essentially eliminated through the use of two observers on watch together (Clarke *et al.* 2003). Working in pairs allows one person to frequently scan the water to 0.5 km ahead, recording birds that could potentially dive before being counted within the 300 m strip-width usually being surveyed (reviewed in Spear *et al.* 2005). Nevertheless, in the present study, multiple observer teams were used during only 41% of surveys. Based on our experience during at-sea surveys, we estimate that the effect of murrelets diving ahead of survey craft resulted in a 5%–10% reduction in number of birds detected. When adjustments for use of single observers are applied to 59% of survey data, we estimate that Xantus's Murrelets were undercounted by about 16%.

A third biasing factor unaccounted for in our analyses was the potential overcounting effect of including unknown numbers of *craveri* with *hypoleucus/scrippsi*. To our knowledge, the only information available on the proportion of *craveri* to *hypoleucus/scrippsi* off the Pacific coast is from pelagic surveys in Monterey Bay, California, indicating that *craveri* make up about 7% of the total number of the two species during the nonbreeding season (S. Terrill, pers. comm.). Although Monterey Bay is in the northern part of the *craveri* nonbreeding range, we have assumed that the 7% value represents a rough average for the entire study area and applies throughout the nonbreeding season. In the nonbreeding season, the number of *craveri* is very low to zero from northern California to central British Columbia, but possibly greater in the SCB and off central Baja California than in Monterey Bay. During the breeding season, *craveri* are rare off central California (LBS & DGA, pers. obs.), but regular off the west coast of Baja California. Therefore, we have assumed that *craveri* accounted for 7% of murrelets surveyed on the Pacific coast of North America during the nonbreeding

season and 5% during the breeding season. Considering negative and positive biases, we believe that our counts of Xantus's Murrelets were underestimated by about 10% during both seasons.

Distribution at sea

During the breeding season, Xantus's Murrelets occurred from northern Oregon to southern Baja California, although they were concentrated in the SCB (Fig. 8). During the nonbreeding season, they were more uniformly dispersed from southern British Columbia to southern Baja California, with the largest concentration off northern Baja California and Point Conception to Cape Mendocino. Moderate densities occurred off Oregon, and low densities occurred off western Washington and the west coast of Vancouver Island, British Columbia. Our northernmost at-sea observation was at 52.5°N (132.7°W, 10 August 2000), similar to latitudes in other northernmost records (Carter *et al.* 2000, 2005; K. Morgan, unpubl. data). During the breeding season, densities of Xantus's Murrelets were low south of Punta Eugenia, Baja California (*c.* 28°N), slightly north of southernmost breeding colonies at San Roque and Asunción Islands (Drost & Lewis 1995). However, in the nonbreeding season, at-sea observations increased south of Punta Eugenia. Although those observations indicated some dispersal to the south, occurrence of these murrelets off southern Baja California is infrequent. The most southern historical records (Howell & Webb 1995, Carter *et al.* 2005) are from Cabo San Lucas (23°N) and Magdalena Bay (24°N), and our most southern record was a pair 35 km off Alijos Rocks (240 km west of Magdalena Bay; 24°N).

Relatively high densities in the inner part of the SCB during the breeding season match known foraging areas from southern California colonies (Whitworth *et al.* 2000, Mason *et al.* 2004). However, relatively high densities of murrelets in offshore waters of the SCB and northern Baja California during the breeding season (Fig. 8) have not previously been documented, and murrelet distribution likely extends further offshore beyond surveyed areas. Oceanographic features and prey resources associated with this concentration need to be better studied. High offshore densities in the region may reflect

- extensive offshore foraging at distances of 150–500 km from Guadalupe Island or other Baja California colonies, given low densities near Baja California colonies;
- early northward dispersal movements of some birds from central Baja California colonies before flightless molt in June–August;
- offshore movements of murrelets from southern California and Baja California shortly after departure from colonies, especially during the at-sea chick-rearing period.

Murrelets attending SCB colonies do not forage more than 100–150 km from colonies (Whitworth *et al.* 2000, Mason *et al.* 2004). Localized high densities near Alijos Rocks (*c.* 25°116'N; Fig. 8) in the breeding season may reflect localized foraging conditions or undocumented breeding by a few pairs at these little-visited small offshore rocks.

In the nonbreeding season, the concentration of murrelets between Point Conception and Cape Mendocino has been recognized for some time (Briggs *et al.* 1987). Northward dispersal of murrelets after breeding likely reflects use of abundant prey resources on the continental shelf, although diet during this time of year and in this region has not been examined (Whitworth *et al.* 2000, Hamilton *et al.*

al. 2004). The large concentration of murrelets off northern Baja California in the nonbreeding season (Fig. 8) has not been noted previously. Oceanographic features and prey resources associated with this concentration need to be better studied. This concentration also may partly reflect variation in timing of movements of birds from Baja California colonies. Delayed northward movements for some murrelets may occur after breeding and after flightless molt, which occurs between June and August (Drost & Lewis 1995). Early southward movements to attend central Baja California colonies prior to breeding typically occurs before 15 March (Keitt 2005, Wolf *et al.* 2005). Thus, we suspect that this concentration may be less distinct in the middle of the nonbreeding season. The occurrence of substantial numbers of murrelets off Oregon, Washington and British Columbia in late summer and fall has previously been recognized, although poorly described in earlier studies (Wahl *et al.* 1993, Nehls 2003). This study clearly shows that the nonbreeding range of the Xantus's Murrelet regularly extends north from California to central British Columbia.

Habitat affinities and ENSO effect

Xantus's Murrelets were most abundant over the upper continental slope (see also Briggs *et al.* 1987). When dispersed away from breeding areas, murrelets were associated with warmer, lower-salinity waters characteristic of the main flow of the California Current. This pattern was consistent within any given year regardless of larger-scale oceanographic conditions. For example, murrelet densities off central California were highest during the ENSO years of 1992 and 1997–1998, but their tendency to disperse north was not significantly related to the ENSO anomaly index. This lack of a relationship is surprising because more birds might be expected to disperse north during warm-water ENSO years, when lower breeding effort and success leads to earlier dispersal from colony areas (Hunt & Butler 1980, Drost & Lewis 1995, Whitworth *et al.* 2000, Roth *et al.* 2005). However, effects of ENSO conditions in any one year often differ between different parts of the California Current, and murrelets seem able to find adequate prey in more southern waters (although not necessarily within foraging distance of colonies) during most years through wide-ranging generalist foraging behavior (Whitworth *et al.* 2000, Hamilton *et al.* 2004, Roth *et al.* 2005).

Most habitat variables were interrelated and significantly correlated with Julian date (Table 2). We found that murrelet densities in central California increased with date over much of the annual cycle (Fig. 5). Thus, seasonal movements of the population, as opposed to habitat selection *per se*, probably account in part for the strong relationships to oceanographic conditions depicted in Fig. 6. For instance, murrelet densities increased with increasing SST and thermocline strength, while Julian date was also positively correlated with those variables. Likewise, murrelet density decreased with thermocline depth and Julian date was negatively correlated with thermocline depth. In contrast, murrelet densities were higher in low-salinity waters, whereas salinity and Julian date were positively correlated. The latter outcome supports our conclusion that Xantus's Murrelets actively choose the lower salinity waters of the main California Current (as suggested earlier). Other indications of habitat selection in our study remain hypothetical and further testing is needed.

Population estimates

CVs for population size estimates indicated that GAMs performed well in modeling murrelet distributions at sea, particularly for the SCB

during the 1999–2001 period, and for the entire population during the nonbreeding season. Population size in the SCB during the 1975–1978 and 1999–2001 periods appeared to be relatively stable. Our best, uncorrected, estimate for 1975–1978 was 11 350 and was 12 600 for 1999–2001 (95% CI for both estimates: 7500–15 500). If corrected for a 10% negative bias, respective estimates become 12 500 and 13 900 (95% CI: 8250–17 000). Mason *et al.* (2004) similarly estimated $13\,855 \pm 3079$ birds in May 1999–2001 for the SCB, but found that mean density in April–June 1975–1983 (0.08 ± 0.03 birds/km²) was 125% lower than in May 1999–2001 (0.18 ± 0.04 birds/km²). However, differences in transect locations and timing of surveys between studies may account partly for differences.

Although estimates of population size between 1975–1978 and 1999–2002 were similar, distribution in the SCB differed between the two periods. During 1975–1978, murrelets concentrated in two areas (adjacent to Santa Barbara Island and the Coronado Islands), but only the concentration near Santa Barbara Island persisted in 1999–2002 (Mason *et al.* 2004; the present study). Lower numbers associated with the Coronado Islands were balanced by higher numbers associated with Santa Barbara Island. Higher numbers near Santa Barbara Island do not reflect population increase at this colony, which has been declining over the past two decades (Carter *et al.* 1992, Sydeman *et al.* 1998, Whitworth *et al.* 2003b). It is not likely that birds from the Coronado Islands began foraging near Santa Barbara Island during the latter period, because the two islands are 180 km apart and beyond suitable foraging distance from the Coronado Islands (Whitworth *et al.* 2000). Lower numbers near the Coronado Islands also do not reflect population decline at that colony. Although cats had reduced numbers of murrelets at Coronado North Island by 1990 (RLP, pers. comm, in Drost & Lewis 1995), breeding murrelets at the other three Coronado Islands were not affected by cats, and murrelets have likely increased at Coronado North Island since cat eradication in the early 1990s (McChesney & Tershy 1998, Whitworth *et al.* 2003c, Keitt 2005). We suspect that differences in survey timing and variation in use of foraging areas likely led to different distributions between the two periods and may have masked the population decline noted at the relatively large Santa Barbara Island colony. Specifically, 1975–1978 surveys occurred, on average, a month earlier and over a considerably longer part of the breeding season than did 1999–2001 surveys (i.e. 15 April \pm 27 days vs. 15 May \pm 2 days). In addition, prey availability and distribution in the SBC, especially for the Northern Anchovy *Engraulis mordax*, also has changed (Jacobsen & Barnes 1994). Birds from Santa Barbara Island foraged further from the colony in 1995–1997 than in 1975–1977 (Hunt *et al.* 1979, Whitworth *et al.* 2000), and birds from the Coronado Islands now appear to forage mostly south of the US–Mexico border, in waters outside the SCB survey area (Fig. 8, Mason *et al.* 2004).

Although temporal trends in population size and distribution in the SCB may be confounded by several factors, we found no evidence for a trend among birds during breeding season surveys in central California (1985–2003; see also Hyrenbach & Veit [2003], who found no trend over an 11-year period embedded within our time series). If global breeding populations had declined to a great degree, we would have detected a decline in numbers in central California, assuming that patterns of nonbreeding distribution had not changed. Our results for the SCB and central California are important, not only from localized perspectives (see below), but also when assessing total population size. SCB estimates represent the average across 29 years (1975–2003) in one of two primary breeding areas,

the other being central Baja California (i.e. Guadalupe and San Benito Islands). In the SCB, population decline has been noted at Santa Barbara Island, increase is suspected at the Coronado Islands, and trends at other colonies are poorly known between 1975 and 2001 (Carter *et al.* 1992, unpubl. data; Sydeman *et al.* 1998; Whitworth *et al.* 2003a, 2003b, 2003c, 2005b; Keitt 2005).

Despite the decline at Santa Barbara Island, it is encouraging that the overall SCB population has not declined below 1975–1978 levels. Population increase is expected to occur at Anacapa Island over the next two decades, following rat eradication in 2002 (Whitworth *et al.* 2005a). However, impacts that lead to decline may occur at the Coronado Islands from the planned construction and operation of a liquid natural gas terminal within the next decade (Whitworth *et al.* 2003c, 2005b). Given the difficulty of censusing colonies and the varying conservation issues, the assessment of overall SCB population condition has been problematic, and declines at Santa Barbara Island have been incorrectly considered by some biologists and managers to reflect the entire SCB population. The present study has shown that the SCB Xantus's Murrelet population is relatively stable at present; however, a long-term monitoring program is needed to better assess trends and conditions at each breeding colony.

Our best, uncorrected, estimate for the number of Xantus's Murrelets at sea is 36 100 birds during the nonbreeding period, and 24 500 birds during the breeding period. When corrected for a 10% negative bias in count data, these estimates are 39 700 and 27 000 birds, respectively. Using the same adjustment, 95% CIs for minimum and maximum estimates of numbers of *scrippsi* and *hypoleucus* are about 30 900–48 100 birds and 18 300–39 100 birds during the respective periods. Our estimate for the nonbreeding period (39 700 birds) is about 25% higher than the maximum global population estimate (30 000) derived from colony-based surveys (Springer *et al.* 1993). This discrepancy is likely due to the difficulty of making population estimates based on colony counts of crevice-nesting birds.

Our estimates of the overall population size differed from estimates based on colony counts, but our estimate of the number of breeding birds is similar to that from the colony-based estimates of 10 000–20 000 breeding birds (Carter *et al.* 2000, Burkett *et al.* 2003, Keitt 2005). While the proportion of nonbreeding adults and subadults in at-sea populations of Xantus's Murrelets is not known, we assume 50%–60% for the nonbreeding period, as found in many other species of seabirds: Ancient Murrelet *Synthliboramphus antiquus*, Adélie Penguin *Pygoscelis adeliae*, Western Gull *Larus occidentalis* and Manx Shearwater *Puffinus puffinus* (Ainley 1978, Spear *et al.* 1987, Brooke 1990, Gaston 1992). Using a value of 45% for breeding adults during the nonbreeding period, we estimate a global breeding population of about 17 900 birds. Using ratios from 95% CIs calculated in the present study (Table 3), minimum and maximum estimates are 13 900 and 21 000 birds respectively.

Crevice-nesting seabirds are especially difficult to census at their colonies. The application of GAMs to at-sea survey data to provide accurate population estimates is a powerful way of monitoring such populations. Estimating population levels and trends over time is critical for the conservation of seabirds like Xantus's Murrelets that are highly restricted in range and are faced with threats to their breeding populations at colonies.

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STATUS OF XANTUS'S MURRELET AND ITS NESTING HABITAT IN BAJA CALIFORNIA, MEXICO

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SUMMARY

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A preliminary survey was conducted in 1999 to establish the status of the Xantus's Murrelet *Synthliboramphus hypoleucus* in Baja California, Mexico. Seven island groups with prior evidence of breeding (Coronado, Todos Santos, San Martín, San Jerónimo, San Benito, Asunción and San Roque) and two potential breeding islands without prior evidence of nesting (Natividad and Adelaida) were examined. In 2004, additional work was conducted at Afuera Islet off Guadalupe Island. Presence of murrelets was detected through nest searches and by rough estimation of birds in nocturnal at-sea congregations using boat-based and land-based vocalization counts. Vocalizations were heard at six island groups (Coronado, Todos Santos, San Martín, San Jerónimo, San Benito and Guadalupe) and nests were found at four island groups (Coronado, San Jerónimo, San Benito and Guadalupe). Land-based and boat-based vocalization surveys both detected presence or apparent absence of murrelets at potential nesting islands, although boat-based vocalization rates were higher on average. Vocalization surveys cannot readily be converted to breeding population estimates, but overall population size of murrelets in Baja California appears to about 2300 pairs (range: 1000–4000 pairs), similar to previous estimates. Historically, nonindigenous mammals were introduced to most islands in Baja California; recent progress in removing introduced mammals should benefit Xantus's Murrelets.

Key words: Baja California, conservation, nesting habitat, predation, status survey, *Synthliboramphus hypoleucus*, Xantus's Murrelet

INTRODUCTION

Xantus's Murrelet *Synthliboramphus hypoleucus* is a small alcid that breeds only on islands off southern California, USA, and northwestern Baja California, Mexico (Fig. 1; Drost & Lewis 1995). The bird's small global population, restricted range, population decline, loss of several breeding colonies, human disturbance at remaining colonies and potential mortality from oil spills have raised concerns about the long-term survival of the species (Hunt *et al.* 1981; Carter *et al.* 1992, 2000; Drost & Lewis 1995, McChesney & Tershy 1998; Sydeman *et al.* 1998). Introduced mammalian predators, especially feral cats (*Felis catus*) and black rats (*Rattus rattus*), have caused declines or extirpations at several islands in the United States and Mexico (Drost & Lewis 1995, McChesney & Tershy 1998, Sydeman *et al.* 1998). High levels of predation by native predators (Deer Mouse *Peromyscus maniculatus* and Barn Owl *Tyto alba*) are also affecting the largest US colony at Santa Barbara Island (Murray *et al.* 1983, Carter *et al.* 1992, Drost & Lewis 1995). Xantus's Murrelet is listed as Threatened in California (2004), "highest priority species at risk" by the Waterbird Society, Vulnerable by the International Union for the Conservation of Nature (IUCN), and Threatened in Mexico under Norma Oficial Mexicana NOM-Ecol-059.

Population estimates for Xantus's Murrelets at colonies are imprecise because murrelets breed mainly in steep coastal habitats inaccessible to researchers, and because murrelets arrive and depart from colonies during the night. Colony-based estimates suggest a global population of 5000 to 10000 breeding pairs (Drost & Lewis 1995, Burkett *et al.* 2003). Recent analysis of at-sea survey data yielded an estimate of 37000 birds, including breeding and nonbreeding individuals (Karnovsky *et al.* 2005). Assuming

50%–60% nonbreeders, that estimate was consistent with a global breeding population of 9000 pairs (Karnovsky *et al.* 2005). Colony-based population estimates for Mexico are based mostly on historical accounts or anecdotal observations; no systematic surveys have ever been conducted. Prior work has furnished estimates of 2000–5000 pairs (Drost & Lewis 1995; H. Carter, pers. comm.). Analysis of at-sea surveys during the breeding season indicated that about 11000–12000 birds occur in Baja California, making no correction for birds attending colonies (Karnovsky *et al.* 2005). That estimate also is consistent with 2000–5000 breeding pairs in Baja California, or roughly half of the global population.

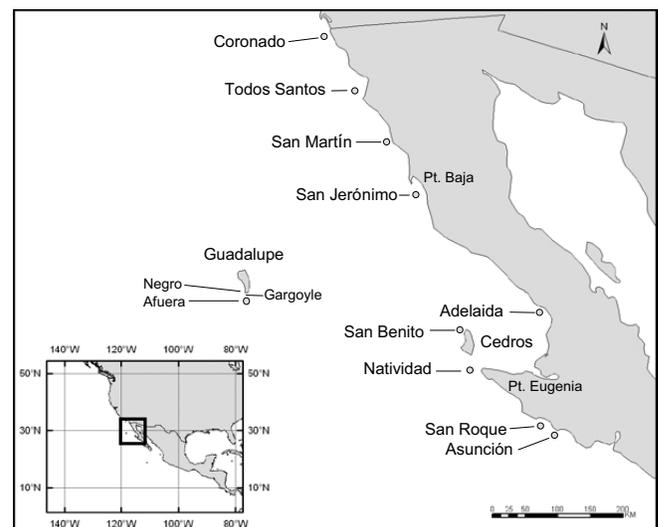


Fig. 1. Map of Xantus's Murrelet breeding islands and other islands surveyed in Baja California, Mexico, in 1999 and 2004.

Because the status of Xantus's Murrelet in Mexico is poorly known—but a large part of the global population probably occurs there—surveying these islands to assess current breeding activity is a priority (Drost & Lewis 1995). Additionally, in light of the recent efforts of Island Conservation (US nongovernmental organization) and the Grupo de Ecología y Conservación de Islas (GECI, a Mexican organization) to remove introduced mammals from islands in northwest Mexico, it is important to summarize the present status of introduced species and threats to Xantus's Murrelets in the region.

From February through July 1999, all Baja California islands with prior evidence of Xantus's Murrelet breeding, except Guadalupe and its offshore islets, were surveyed by the author and others using nest searches and nocturnal vocalization counts. Nest searches on Afuera Islet off the south end of Guadalupe Island were conducted in May 2004. In addition, surveys were conducted in 1999 at two islands without prior evidence of breeding. Cedros, a large island with potential nesting habitat and numerous offshore islets, was not surveyed. At each island, the primary goals were

- to establish presence or absence of breeding Xantus's Murrelets.
- to obtain a preliminary estimate of population size.
- to record introduced predators that may pose a threat to murrelets.
- to assess potential threats to murrelets from human use of the islands.

Additional data collected by the author and by GECI personnel during visits to some islands between 1996 and 2003 are also summarized.

METHODS

Study area

Eleven islands or island groups off the west coast of Baja California provide known or potential nesting habitat for Xantus's Murrelet (Fig. 1). Coronado (4 islands), Todos Santos (2 islands), San Martín and San Jerónimo islands are located within the southern region of the Southern California Bight in waters dominated by the California Current. San Benito (3 islands), Cedros, Natividad, Adelaida (also known as Elide), San Roque and Asunción islands are located in a region characterized by persistent winds favorable to upwelling. Intensive upwelling occurs year-round near the coastal prominences of Punta Baja (north of San Jerónimo) and Punta Eugenia (south of Cedros Island) (Parrish *et al.* 1981). Guadalupe, an oceanic island located 250 km offshore, is less influenced by coastal upwelling.

All islands in the region are Mexican federal property with restricted access. Three islands, Natividad, San Roque and Asunción, are located within the nuclear zone of the Vizcaino Biosphere Reserve, a designation affording the highest protected status in Mexico and roughly equivalent to a U.S. national park. Guadalupe Island was designated as a wildlife reserve in 1922, primarily to protect marine mammals. Increased protection was afforded when the island was designated a biosphere reserve in June 2005. A proposal to create a biosphere reserve protecting other islands in the region (Coronado, Todos Santos, San Martín, San Jerónimo, Adelaida, San Benito and Cedros) was submitted to the Mexican government and was officially accepted and distributed for public comment in summer 2005.

Survey approach

Between February and July 1999, nest searches and vocalization surveys were conducted at nine islands or island groups: Coronado, Todos

Santos, San Martín, San Jerónimo, Adelaida, San Benito, Natividad, Asunción and San Roque (Fig. 1). Although breeding phenology is not well known in Mexico, an attempt was made to survey each island early in the breeding season, when colony attendance and vocal activity is expected to be high. The San Benito Islands were surveyed on three occasions to assess nesting phenology. At Guadalupe, nest searches were conducted on Afuera Islet in May 2004.

Nest searches

Xantus's Murrelets nest primarily in rock crevices, but also under dense shrubs and in human-created structures (Murray *et al.* 1983, Carter *et al.* 1992). Apparently suitable habitat was searched using handheld flashlights to look into potential nest cavities. Effort was concentrated on crevice habitat, but vegetation was checked opportunistically. In general, search effort was concentrated in scree fields, along the bases and tops of cliffs, and in caves. Some islands, such as San Benito, were searched more thoroughly because of easy access; other islands with large areas made inaccessible by terrain or the presence of breeding pelicans and cormorants, were poorly searched (e.g. Todos Santos and Coronado islands). Nest searches were made during day and night. When a nest was found, nest contents and site characteristics (distance of nest from crevice entrance, crevice dimensions, substrate and distance to ocean) were estimated and recorded. Active and inactive nests were recorded, and the nest totals reported for each island include both categories. Active nests contained adults, chicks or whole, fresh, unattended eggs. Inactive nests contained old egg shells or membranes that indicated nesting in a previous year. When clearly viewable, adult birds at nests were identified to subspecies using facial plumage patterns (Jehl & Bond 1975). The number of person-hours of search effort on each island was recorded.

Vocalization surveys

Nocturnal attendance and vocalizations by Xantus's Murrelets in at-sea congregations are thought to be associated with nesting activity (Carter *et al.* 1996; Whitworth *et al.* 2002, 2003a; H. Carter, unpubl. data). At Santa Barbara Island, vocalizing was most common in mid-May, coincident with the hatching period (Murray *et al.* 1983). Nightly peaks of vocal activity were evident 2–3 hours after dark (22h00–24h00) and just before dawn (Murray *et al.* 1983). More recent work at several colonies in California detected no consistent peaks in vocalization activity (H. Carter and D. Whitworth, unpubl. data).

Vocalization surveys reveal presence or absence and relative abundance of birds in inaccessible habitats with relatively low cost and effort. They are most valuable where surveys cannot be conducted using other techniques. In 1994–1996, standardized vocalization surveys were used to assess many inaccessible breeding areas that had not been previously surveyed in the Channel Islands, California, and at the Coronado Islands, Baja California (Carter *et al.* 1996; H. Carter, unpubl. data). For each vocal detection in a 15-minute period, time (to the nearest second), direction (to the nearest cardinal region—N, NE, E, etc.) and relative distance (designated near, medium or far) was noted by a designated observer and recorded by an assistant. A vocal detection was defined as a single call or a continuous series of calls separated by less than 5 seconds. During any one survey, a single bird could be responsible for multiple detections, thus the number of detections does not directly indicate the number of birds in the area.

Vocalization surveys in 1999 were conducted in open fiberglass skiffs (7-m with 40–65 hp outboard engines). Boat surveys were

conducted about 100 m from shore with engine off and wind speed < 15 knots. When skiffs were not available, surveys were conducted from shore in areas with little wave noise. Surveys were conducted on all sides of islands if possible. Survey locations were selected using a map, giving priority to coves and areas adjacent to apparently suitable nesting habitat. All survey locations were marked with a hand-held GPS. Most surveys were conducted between 22h00 and 02h00 (PST or PDT), and all surveys occurred between 90 minutes after sunset and 30 minutes before sunrise.

RESULTS

Coronado Islands

Background

Murrelets are known historically to breed on all four islands. Breeding was first noted in 1893 (Whitworth *et al.* 2003b, Carter *et al.* 2005), and recent estimates (prior to 1999) ranged from 325 to 1125 pairs (Drost & Lewis 1995; Carter *et al.* 1996). Feral cats formerly occurred on North and South islands and are likely responsible for large population declines from historical levels. Cats were removed from both islands (Table 2), and populations may be recovering. Goats and burros were removed from South Island in 2003 (Table 2).

South Island (226 ha, 2.8 km long, 204 m high) supports a small Navy encampment (about 10 personnel) and one permanent lighthouse keeper. North Island (80 ha, 1.6 km long, 136 m high), Middle Island (32 ha, <1.6 km long, 76 m high) and Middle Rock (22 ha, <1.6 km long, 31 m high) are uninhabited. The islands are steep and sparsely vegetated. High-quality scree and boulder field

nesting habitat occurs on all islands, especially along the shoreline, with the east sides of North and South Islands apparently providing the most extensive habitat.

1999 Results

During 11–18 April 1999, eight nests were found and nine vocalization surveys were conducted. Six nests were found in 13.5 person-searching hours (psh) on North Island (0.4 nests/psh). On South Island, two active nests were found in 4 psh (0.5 nests/psh, Table 1). Middle Island and Middle Rock were not searched. Ground searches were conducted on the east side of North Island around the landing cove, upslope through the “amphitheater” to the top ridge and on the lower slopes south of the landing cove. All nests were found on the east side of the island in rocky, talus substrate from about 5 m to 50 m elevation. The best habitat on the North Island appeared to be in the “amphitheater” above the landing cove and just south of the landing, where small caves and natural crevices were abundant. The southern end of North Island also appeared to have excellent habitat, but was not surveyed because of difficult access on foot. All nests on South Island were located in a small boulder field west of the north-end Navy station between 5 m and 20 m above the water. Abundant habitat was also evident in other areas of South Island and on Middle Island and Middle Rock. Two vocalization surveys were conducted by boat at North Island, and four boat and three land surveys were done at South Island. Detection rates at Coronado Islands were higher than at any other location surveyed in 1999, with an average of 180 detections per survey (maximum of 253 detections in the channel between South and Middle islands).

TABLE 1
Xantus's Murrelet vocalization surveys conducted at islands in Baja California in 1999

Island	Dates visited	Boat surveys				Land surveys			
		n	\bar{X} ^a	SD	Range	n	\bar{X} ^a	SD	Range
Coronado North	12, 17–18 April	2	163	—	158–168	—	—	—	—
Coronado South	11–12, 18 April	4	187	60	109–253	3	148	37	121–191
Todos Santos North	7, 9 April	1	1	—	—	—	—	—	—
Todos Santos South	2–9 April	5	21	16	7–46	4	19	26	0–56
San Martín	21–23 April	—	—	—	—	6	2	4	0–10
San Jerónimo	23–26 April	—	—	—	—	5	31	36	0–86
San Benito East	25–28 February	4	28	16	14–44	2	23	—	11–13
	3–4 May	3	37	12	23–48	—	—	—	—
San Benito West	23–25, 28 February	3	21	18	3–40	8	12	13	0–40
	1–3 May	3	46	33	17–82	3	47	49	27–77
	28 June–3 July	6	2	4	0–10	—	—	—	—
San Benito Middle	26, 28 February	2	14	—	1–28	—	—	—	—
Natividad Island	6–8 May	—	—	—	—	1	0	—	—
San Roque	4–5 March	—	—	—	—	4	0	—	—
Asunción	3–4 March	—	—	—	—	3	0	—	—

^aMean detections per survey.

TABLE 2
Status of Xantus's Murrelets and introduced mammals on islands in Baja California

Island	Nesting status		Nests this study ^a	Introductions	
	Historical	Current		Species, dates ^b	Current status ^c
Coronado North	Confirmed	Confirmed	6 (1)	Cats 1970s/1980s	Removed 1995/96
Coronado South	Confirmed	Confirmed	2 (2)	Cats 1908	Removed
				Goats	Removed 2003
				Burros	Removed 2003
Todos Santos North	Confirmed	Present	0	Cats 1923, 1970	Removed 1999
				Rabbits	Removed 1999
Todos Santos South	Confirmed	Present	0	Cats 1923, 1970	Removed 1998
				Rabbits	Removed 1998
				Burros	Removed 2003
San Martín	Suspected	Present	0	Cats	Removed 1999
				Rabbits	Died out
San Jerónimo	Confirmed	Confirmed	5 (3)	Cats	Removed 1999
San Benito East	Confirmed	Confirmed	16 (7)	Cats	Removed 1998
				Rabbits 1994–96	Removed 1998
San Benito Middle	Confirmed	Confirmed	3 (3)	Cats	Removed 1998
				Rabbits 1994–1996	Removed 1998
San Benito West	Confirmed	Confirmed	9 (3)	Cats	Died out
				Rabbits 1991	Removed 1999
				Burros	Removed 2004
				Goats	Removed 1998
Cedros	Possible	Not surveyed in this study	—	Goats (1800s)	Present
				Cats	Present
				House mice	Present
				Feral dogs	Present
				<i>Rattus</i> spp.	Present
Natividad Island	Possible	No detection	0	Cats 1900s	Removed 2000
				Goats 1990s	Removed 1997
				Sheep 1990s	Removed 1997
				Dogs 1927	Present ^d
				Ground squirrel ^e	Present
San Roque	Suspected	No detection	0	Roof rats	Removed 1994
				Cats 1970s	Removed 1994
Asunción	Confirmed	No detection	0	Cats	Removed 1994
Guadalupe (main)	Confirmed	Not surveyed	—	Goats (1800s)	Removal in progress
				Cats	Present
				House mice	Present
				Feral dogs	Present
(Afuera)	Confirmed	Confirmed	35 (24)	None	None
(Negro)	Confirmed	Confirmed	Several hundred	None	None
(Gargoyle)	No record	Confirmed	4 (0)	None	None

^a Total nests found in this study; number of active nests in parentheses.

^b Approximate dates of historical introduction or earliest record.

^c Data from Island Conservation database (www.IslandConservation.org).

^d In March 2002, only three dogs remained on Natividad Island, down from a high of approximately 30 dogs in 1998.

^e *Ammospermophilus leucurus*.

Todos Santos Islands

Background

Kaeding (1905) reported murrelets as “fairly common on and about” the islands. The first reported nesting was from 1940, when one nest was found and eggs collected (Carter *et al.* 2005). Feral cats were present as early as 1923, and Jehl & Bond (1975) suggested that cats had extirpated murrelets from the island.

South Island (127 ha, 95 m high) is mostly flat on top and ringed by cliffs. North Island (62 ha, 17 m high) is relatively flat-topped with north-side cliffs and beach access along most of the south side. An abalone cultivation facility on South Island housed about 20 personnel in 1999. That facility has since reduced operations, and in 2003 only one caretaker remained. A small illegal lobster fishing camp with two structures on the south end of South Island was removed in 2004 by GECI and the Mexican Navy. North Island has a lighthouse keeper and two Navy personnel. Rabbits and cats were removed from North Island and South Island in 1998. Burros were removed from South Island in 2003 (Table 2).

1999 Results

During 2–9 April 1999, no nests were found in 20 psh, but murrelet presence was detected during 10 vocalization surveys. Terrain on South Island was searched except for cliffs along the east, west and south sides. The base of east-side cliffs was explored by kayak and on foot. Search effort was concentrated in rocky habitat and to a lesser extent in the shrubs on top of the island. There was abundant shrub habitat, but the typical plant structure did not appear to provide enough cover to encourage nesting. On North Island, the north and east coastlines were searched, mainly in rocky habitats. One boat vocalization survey was conducted on North Island and nine surveys (five by boat, four by land) were done at South Island. The range of vocal activity was 0–56 detections per survey. Land and boat surveys averaged 19 and 18 detections, respectively. The survey with 56 detections was a land survey on the east side of South Island, above the fishing camp cove. A boat survey conducted adjacent to this point (three nights and 80 minutes earlier—i.e. 23h00 versus 00h20) had 13 detections.

San Martín Island

Background

Kaeding (1905) reported murrelets as “fairly common on and about” the island and nesting has long been presumed, though historical records of nests are lacking (Carter *et al.* 2005). Jehl & Bond (1975) suggested that feral cats had extirpated murrelets from the island. The island (300 ha, 1.6 km long, 151 m high) is the cone of an extinct volcano and has many lava tubes on its flanks. Steep cliffs occur around the north and west sides; uplands are covered with dense brush and sharp lava boulders. Traversing the island off trail is difficult. There is one fishing camp with about 20 buildings and 5–10 seasonal fishermen.

1999 Results

During 21–23 April 1999, no nests were found in 4.0 psh, but murrelets were detected in vocalization surveys. Search effort targeted the coastline; an intensive survey of the entire island was not conducted because of the rough terrain. Apparently suitable habitat was present around much of the island, including many crevices in lava rocks and in small caves along the cliffs. Cassin's Auklet *Ptychoramphus aleuticus* nests were found in crevices, especially those with some soil, which allowed auklets to modify the nest entrances. Six land-based vocalization surveys were

conducted, results ranging from 0 to 10 detections. The survey with 10 detections was located on the southwest side of the island. No boat-based surveys were conducted. Interestingly, areas where murrelets were heard offshore were adjacent to areas apparently not used by Cassin's Auklets.

San Jerónimo Island

Background

Kaeding (1905) reported murrelets as “fairly common on and about” the island. Breeding was first documented in 1932 when one nest was found and the eggs collected (Carter *et al.* 2005). Jehl & Bond (1975) suggested that feral cats had extirpated murrelets from the island. The island is small and low (67 ha, 1.2 km long, 40 m high) with sandy soil and little vegetation. It supports a large colony of Cassin's Auklets (>10 000 birds; Wolf 2002). A permanent fishing village with about 15 buildings and 30 fishermen is located on the southwest side. In the late 1990s, a guano mining operation displaced a large colony of Brandt's Cormorants *Phalacrocorax penicillatus* and destroyed hundreds of Cassin's Auklet burrows. This activity was subsequently stopped, but cormorants have yet to recolonize. The guano mining operation is unlikely to have significantly impacted Xantus's Murrelets.

1999 Results

During 23–26 April 1999, five nests were found and murrelets were also detected in vocalization surveys. Four nests were located in 8 psh (0.5 nests/psh), three within the fishing village (two under woodpiles and another inside a shack). The other two nests were located in small caves just above the shoreline. Two nests contained adults, two nests had unattended eggs, and one nest had fresh-hatched shell fragments. In addition, six adult birds were seen on the ground at night. All six, plus two incubating birds, were identified as *S. h. scrippsi*. Five land-based vocalization surveys averaged 31 detections, ranging from 0 to 86 detections. Highest vocal activity occurred on the south side of the island, in the cove fronting the village.

San Benito Islands

Background

Historically, breeding was first noted in 1896 (Carter *et al.* 2005); Drost & Lewis (1995) estimated 500 breeding pairs. More than 2 million seabirds of 13 species breed in this island group (Wolf 2002). The three San Benito Islands encompass about 640 ha. The largest, West Island (200 m high), supports a seasonal fish camp with about 35 buildings and up to 70 people at the height of abalone season. The islands are dry, with a combination of scree and sandy soil habitat. All habitat was accessible, excluding some steep cliffs on West Island and places where dense colonies of Cassin's Auklets precluded walking. This location is unique in that both subspecies of Xantus's Murrelet and congeneric Craveri's Murrelets *Synthliboramphus craveri* were thought to breed sympatrically on the San Benito Islands (Jehl & Bond 1975). That conclusion was based on captures of birds near the islands, however; and active nests of *S. h. hypoleucus* and Craveri's Murrelet have not been reported previously.

1999 Results

In 1999, 28 nests were found, and murrelets were detected during 34 vocalization surveys. During 23–28 February, 17 nests were found in 58 psh on all three islands (0.4 nests/psh). During 1–4 May, 11 nests were found in 16 psh. The entire perimeter of West Island was explored, except the steep southwest side near a

small light tower. In the island's interior, 5 psh yielded no nests. All nine nests found on West Island were in rocky crevice habitat on the eastern half. Habitat quality (i.e. presence of rock crevices) appeared lower in the western half and interior of West Island than in the eastern half. The best habitat on Middle Island appeared to be an area of boulder scree at the base of a 15-m cliff on the northeast side. One nest was found in a solitary rock outcrop on the east side of Middle Island, and two other nests, at the base of a 10-m cliff on the north side. Sixteen nests were found on East Island, distributed among all sides of the island. The best habitat and most nests were found in and around the rocky ridge running along the south shore. Two nests contained birds with *S. h. hypoleucus* facial patterns—a nest on West Island containing two chicks (25 February) and another on Middle Island containing an adult on two eggs (3 May). Vocalization counts conducted during 23–28 February, 1–4 May and 28 June–3 July averaged 26 detections per survey. May surveys had the highest average detection rates (43 detections/survey, $n = 11$), compared with 17 detections/survey ($n = 9$) in February and 2 detections/survey ($n = 6$) in June and July. The two surveys with highest detections (one land-based, 77 detections; one boat-based, 82 detections) occurred on consecutive nights on West Island. Both were done on the southeast side of the island, near the main landing cove for the fish camp.

Adelaida Island

Background

No evidence of historical breeding is known. This small, low-lying rocky islet (5 ha, 12 m high) has no vegetation. A small shack on the east side has been used as a residence by guano miners in the past. Large numbers of California Sea Lions *Zalophus californianus* haul out on the island. The island is covered in a smooth layer of bird guano and feces from the sea lions. Guano mining may resume on Adelaida in the near future (E. Palacios, pers. comm.).

1999 Results

No nests were found on 7 March 1999. No vocalization surveys were conducted. About 200 small burrows were noted on the island. Forty were checked with flashlights, and only one abandoned egg was found, which was not reachable. Based on the solid white color, size and shape of the egg, it was probably from a Cassin's Auklet or storm-petrel (*Oceanodroma* sp.).

Natividad Island

Background

No evidence of historical breeding is known. The south half of the island consists of stabilized sand dunes that support the world's largest colony of Black-vented Shearwaters *Puffinus opisthomelas* (Keitt *et al.* 2000). Feral cats, present since the early 1900s and removed in 2000, greatly impacted the shearwater colony (Keitt *et al.* 2002, Keitt & Tershy 2003). Cats may have extirpated both murrelets and Cassin's Auklets. The northern half of this moderate-size island (1000 ha, 6.1 km long, 150 m high) is steeper than the more sloping southern half, with numerous drainages cutting into a central plateau in the northern third of the island. Shrub and cactus habitat is common on the northern half. A town of 120 buildings and about 500 fishermen is located on the southwest side of the island. Natividad Island is considered a possible historical breeding site for Xantus's Murrelets (Drost & Lewis 1995).

1999 Results

During 6–8 May 1999, no nests were found in 15 psh, and no murrelets were heard vocalizing at night. Nest search effort was

concentrated on the north end in both shrub and scree habitat. The south end of the island was not searched because past work (see below) had indicated that murrelets did not breed there. One vocalization survey conducted on the middle east coast produced no detections. Murrelet calls were listened for opportunistically while walking at night (11h30–02h00) over a distance of 3 km along the east shore, but no birds were detected. Additionally, during two 4-month seasons of field research by the author (spring and summer of 1997 and 1998), no Xantus's Murrelets were heard. The only murrelet so far encountered on Natividad was a Craveri's Murrelet captured at night on a boat just offshore of the island on 6 May 1997. Photographed in hand, the bird clearly showed the dark underwing linings and facial pattern of a Craveri's Murrelet. It did not have a brood patch and was not yet undergoing primary molt.

Asunción Island

Background

A dead Xantus's Murrelet and egg were reportedly collected in 1977 (R. Osorio, pers. comm., cited in Drost & Lewis 1995)—the only evidence of historical breeding. This small island (67 ha, 1.2 km long, 50 m high) is relatively barren, with a few California Boxthorn *Lycium californicum* shrubs and other low-lying vegetation scattered across the island. Although uninhabited, the island is visited regularly by fishermen. Feral cats destroyed a substantial colony of Cassin's Auklets in the 1970s (McChesney & Tershy 1998).

1999 Results

On 3–4 March 1999, no nests were found in 8 psh, and no murrelets were heard on three vocalization surveys.

San Roque Island

Background

Bancroft (1927) reported breeding murrelets on this small island (79 ha, 1.2 km long, 15 m high), although it is unclear whether they were Xantus's or Craveri's murrelets. Historical guano-mining operations likely impacted murrelets. Rats, probably introduced during guano mining, eradicated breeding Cassin's Auklets (McChesney & Tershy 1998).

1999 Results

During 4–5 May 1999, no nests were found in 6.5 psh, and no murrelets were heard during four vocalization surveys.

Guadalupe Island

Background

Breeding was first reported in 1892 (Carter *et al.* 2005). Nests have not been found on the large main island (26 500 ha, 32 km, 1300 m), which supports a small military garrison (approximately seven personnel) and a fishing cooperative (approximately 70 members). The southern subspecies (*S. h. hypoleucus*) has been documented to breed on two offshore islets: Negro (17 ha, 0.7 km long, 35 m high), with an estimated 200 pairs, and Afuera (68 ha, 1.1 km long, 200 m high), with an estimated 1000–1500 pairs (DeLong & Crossin 1968, Jehl & Everett 1985). No *S. h. scrippsi* have been found breeding at Guadalupe Island. Feral cats, present on the main island since at least 1900, have probably reduced greatly the number of murrelets there. In 1977, Pierson and Riedman reported murrelet carcasses in a cave on the east side of the main island, suggesting that nesting may persist in some places (see Jehl & Everett 1985). In addition, between 2001 and 2003, several cat-killed adult murrelets were found on the south end of the main island (R. Henry, unpubl. data).

2003/04 Results

On 16 May 2004, 35 nests were found on Afuera Islet in 2.75 psh (12.7 nests/hour). Nine nests had incubating adults and 15 nests had freshly hatched eggshell fragments. Eleven nests contained abandoned eggs or old eggshells where it was not possible to determine whether eggs had hatched or not. Fifteen of the 35 nests (43%) were located under shrubs. Afuera Islet was the only site where nesting beneath shrubs was encountered in this study. Several hundred old eggs from previous years (i.e. inside and outside of inactive nest sites) were found on Negro Islet just before the 2003 breeding season. Nesting (four inactive sites with abandoned eggs) was noted on Gargoyle Rock, between the south point of Guadalupe Island and El Toro Islet (D. Barton, K. Lundquist & R. Henry, unpubl. data). Frequent vocalizations were heard at the south end of the main island, but no vocalization surveys were conducted.

Cedros Island

Background

No evidence of historical breeding is known. This large island (37 800 ha, 33 km long, 1200 m high) supports a large military base (several hundred personnel) and a town of 3000 people. Predators (e.g. cats, rats, and dogs) limit potential seabird habitat. However, the island's large size and multiple offshore rocks provide abundant habitat that has never been examined for murrelet nesting.

1999 Results

No nest searches or vocalization surveys were conducted.

DISCUSSION

The status of Xantus's Murrelet in Baja California, Mexico, has been difficult to determine because of the large geographic extent and remoteness of the area, the difficulty of conducting population surveys and insufficient resources. However, heightened interest in assessing population status in Baja California stems from apparent population declines of Xantus's Murrelets elsewhere and increasing threats, both at sea and at breeding islands throughout the species' range (Drost & Lewis 1995; McChesney & Tershy 1998; Carter *et al.* 1992, 2000; Burkett *et al.* 2003). The most important findings from surveys conducted in 1999 and 2004 were these:

- Murrelets currently breed on San Jerónimo Island (based on observed nests) and probably breed on Todos Santos and San Martín islands (based on vocalizations), where it was thought they had been extirpated by introduced mammals (Jehl & Bond 1975, McChesney & Tershy 1998).
- Murrelets continue to breed on Coronado, San Benito and Guadalupe (offshore islets) islands.
- The first nests of the southern subspecies (*S. h. hypoleucus*) were found at the San Benito Islands.

Nest searches

Murrelet nests were found on seven of 14 islands searched. Nest detection rates are not direct indices of nest abundance because terrain and habitat affected greatly the results of nest searching. Searching was easiest on the San Benito Islands (27 nests found) and most difficult on San Martín Island (no nests found). Excluding Guadalupe Island (12.7 nests/psh), nest detection rates were similarly low on all islands where nests were found (0.4–0.5 nests/psh) and seemed more affected by terrain than by abundance of birds. Nest detection did not increase directly with the number of vocalization detections at each island. For example,

nest detection was similar (0.5 nests/psh) on South Coronado Island (187 vocalization detections/survey) and San Jerónimo Island (31 vocalization detections/survey). The highest rate of nest detection occurred on Afuera Islet, where previous observers also reported large numbers of breeding murrelets (DeLong & Crossin 1968, Jehl & Everett 1985). Given the high historical estimates and high nest detection rates in this study, the Guadalupe Island area appears to have the largest population of the southern subspecies (*S. h. hypoleucus*) and possibly the largest breeding population of Xantus's Murrelets anywhere (see also Jehl & Everett 1985). At most colonies, nest searches are not useful for estimating the total breeding population of Xantus's Murrelets, but may be used in the most accessible habitats on certain colonies (e.g. Santa Barbara Island; Carter *et al.* 1992). Nest searches are valuable for confirmation of breeding, assessing nesting phenology, assessing subspecific status and verifying the link between near-shore vocalizations and nesting on the adjacent island.

Vocalization surveys

Murrelet vocalizations were heard at 12 of 15 islands surveyed. All islands with nests found had vocal activity, and three islands on which no nests were found also had vocal activity (San Martín, Todos Santos North, and Todos Santos South). It has been suggested that vocalization activity occurs only near nesting colonies (Carter *et al.* 1996, Whitworth *et al.* 2002). The fact that vocalizations were heard at all the islands where nests were found supports this assertion. The failure to find nests at other islands with vocalization detections does not refute the connection because of the great difficulty of finding nests in inaccessible habitats. Vocalization detection rates were highest on the Coronado Islands in 1999 and were similar to rates reported at the Coronado Islands and at Santa Barbara Island in 1995 (Carter *et al.* 1996; H. Carter, unpubl. data). Whitworth *et al.* (2003b), using spotlight surveys in 2002, also found large numbers of murrelets at the Coronado Islands. Low rates of vocal detection at Todos Santos Islands suggest that small numbers of birds were breeding in non-searched areas. In fact, nests were found on South Island in 2005 (H. Carter & D. Whitworth, unpubl. data). Unfortunately, correction factors are not available to calculate population size of breeding birds from vocal detection rates. Assuming that a generally positive correlation exists between numbers of vocal detections and breeding population size, the Coronado Islands appear to support the largest colony of *S. h. scrippsi* (see also Whitworth *et al.* 2003b).

Boat-based vocalization surveys tended to have higher detection rates than did land-based surveys on three islands where both were conducted. Boat-based surveys averaged 60.2 detections per survey (n = 26), and land-based surveys averaged 39.3 detections per survey (n = 20). Because land-based surveys detected equally well the presence or absence of murrelets in nearshore at-sea congregations, this technique may be an effective way to determine murrelet presence without the need for a boat or for long periods of nest searching.

Breeding phenology at the San Benito Islands

Drost & Lewis (1995) mentioned potential earlier breeding at the San Benito Islands and other southern colonies. At the San Benito Islands, two nests with apparently freshly laid single eggs (clean eggs showing no signs of extended neglect) were found in late February 1999, indicating that the female was at sea forming the second egg (Murray *et al.* 1983). Nests with young chicks were also encountered, which suggested at least some egg laying had occurred

in early-to-mid January 1999 (incubation lasts 27–44 days according to Murray *et al.* 1983). Murrelet activity was higher in May than in February 1999 judging from nest encounter rates (0.68 per hour versus 0.3 per hour) and vocalization rates (43 detections versus 17 detections per survey). Thus, peak colony attendance may have occurred in March–May 1999, as found for colonies in most years in southern California (Murray *et al.* 1983; Drost & Lewis 1995; Whitworth *et al.* 2003a; H. Carter, unpubl. data). In July 1999, vocalizations had tapered off, and the breeding season was mostly finished, as also found in southern California.

In 2002, the breeding season was well advanced in late March, based on a relatively high proportion of birds with brood patches captured at sea at the San Benito Islands (Whitworth *et al.* 2003c). In 2003, breeding at West San Benito Island began in March and continued through July (Wolf *et al.* 2005). At Afuera Islet in 2003, murrelets showed a phenology similar to that at the San Benito Islands in 2003, with birds arriving at the island in January and first nests found in March (R. Henry, D. Barton & K. Lundquist, unpubl. data). At Afuera Islet in 2004, birds were incubating on 12 May, and numerous nests had fresh-hatched shell fragments, suggesting phenology similar to that seen in 2003. In summary, early breeding by at least some birds occurs in the San Benito Islands in some years, and extensive overlap in the timing of breeding occurs throughout the breeding range in many years.

Subspecies of Xantus's Murrelet and Craveri's Murrelet

To my knowledge, the two nests of *S. h. hypoleucus* found on the San Benito Islands are the first nests documented for that location. Previously, the nominate subspecies was surmised to breed on the San Benito Islands, based on the capture of birds in nearshore waters (Jehl & Bond 1975, Drost & Lewis 1995, Whitworth *et al.* 2003c). However, *S. h. scrippsi* was the most frequently encountered subspecies during work at the San Benito Islands in 1999 and 2002 (Whitworth *et al.* 2003c).

Based on at-sea captures and museum specimens, varying ratios of murrelets have been reported for the San Benito Islands:

- 40% *S. h. scrippsi*, 20% *S. h. hypoleucus*, 40% *S. craveri* (n = 17 at-sea captures; DeLong & Crossin 1968)
- 47% *S. h. scrippsi*, 38% *S. h. hypoleucus*, 15% intermediate forms (n = 47 at-sea and museum specimens; Jehl & Bond 1975)
- 61% *S. h. scrippsi*, 32% *S. h. hypoleucus*, 7% intermediate forms (n = 44 at-sea captures; Whitworth *et al.* 2003b)

Since the late 1960s, no Craveri's Murrelets have been documented, and a nest of this species has yet to be found at the San Benito Islands. Past occurrence in this vicinity may reflect postbreeding dispersal from colonies in the Gulf of California. This idea is supported by the relatively late dates of occurrence of Craveri's Murrelets at the San Benito Islands as compared with known breeding phenology in the Gulf of California (DeWeese & Anderson 1975, Carter *et al.* 2005).

Introduced mammals

Introduced mammals occurred in the past on at least 12 of the islands surveyed. Murrelet predators (cats and rats) historically occurred on 10 of the islands, and herbivores (rabbits, goats, sheep, burros) occurred on at least five islands (Table 2). Cats and rats are known to prey on adult seabirds (McChesney & Tershy 1998, Keitt *et al.* 2002, Keitt & Tershy 2003), and researchers have found many cat-killed murrelets on Baja California islands. R. Pitman

reported carcasses of 204 murrelets on Coronado North Island in 1989 and 1990 (Carter *et al.* 1996; McChesney *et al.* 2000). B. Tershy and BSK (unpubl. data) collected more than 50 murrelet carcasses on North Coronado Island in 1994. Introduced predators have had an extensive impact on murrelets in Mexico, possibly causing four island extirpations (Asunción, San Roque, Natividad and Guadalupe [main island]) and significant declines in four island groups (Coronado, Todos Santos, San Martín and San Jerónimo). Extirpations and declines appear to have had greater impact on the southern subspecies, *S. h. hypoleucus*. However, additional surveys are needed to verify potential extirpations and to better determine current population sizes.

Since 1994, GECI and other groups have removed introduced mammals from every murrelet breeding island or island group in Mexico except Guadalupe (Table 2). Currently, introduced mammals occur only on the main island at Guadalupe (cat, dog, goat), Cedros Island (cat, rat, goat and others) and Natividad Island (ground squirrel, dog). The eradication of introduced mammals on the islands has greatly reduced the most significant colony-based threat to the Xantus's Murrelet in Baja California, Mexico. Additional surveys are needed to monitor expected population increases.

Population estimates

Standard methods to estimate populations of Xantus's Murrelets have not been developed, and many current estimates are based on few data. Data obtained in Baja California in 1999 and 2004 suggest that populations remain similar to those previously estimated (e.g. about 2300 breeding pairs; Drost & Lewis 1995). From observations of birds and nesting habitat in 1999 and 2004, preliminary estimates of breeding populations at island groups are Coronado, 750–1500 pairs; Todos Santos, <50 pairs; San Martín, <50 pairs; San Jerónimo, <100 pairs; San Benito, 300–750 pairs. Including a previous estimate of 1000 pairs for Guadalupe Island, I roughly estimate between 2200 and 4000 breeding pairs in Baja California, Mexico, consistent with other estimates of 2000–5000 pairs (see "Introduction"). However, true population size may exceed these estimates, given

- the large numbers of vocal detections and birds counted by Whitworth *et al.* (2003b) during spotlight surveys at the Coronado Islands;
- a potentially protracted breeding season (January through June) on the San Benito Islands in 1999 (affecting this study); and
- the upper confidence limit on population size derived from at-sea surveys (Karnovsky *et al.* 2005).

Future research and conservation actions

Islands on the northwest coast of Baja California provide critical breeding habitat for Xantus's Murrelets. Despite recent efforts to remove introduced mammalian predators and herbivores from some islands, more work is needed. Currently, the main colony-based threats in Mexico are feral cats on Guadalupe Island, the threat of future introductions of cats and rats to nesting islands, and the effect of bright lights at colonies. In addition to direct conservation actions, further research and surveys are needed to develop a better understanding of the breeding biology and status of Xantus's Murrelets on Baja California islands. Future surveys should concentrate on Guadalupe and Cedros islands. Standardized methods for determining population sizes and assessing changes in breeding populations are needed.

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XANTUS'S MURRELET BREEDING RELATIVE TO PREY ABUNDANCE AND OCEANOGRAPHIC CONDITIONS IN THE SOUTHERN CALIFORNIA BIGHT

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SUMMARY

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We investigated the effects of temporal variability in prey abundance and oceanographic conditions on Xantus's Murrelet *Synthliboramphus hypoleucus* breeding on Santa Barbara Island, California, USA, from 1983 to 2001. We used estimates of prey abundance from California Cooperative Oceanic Fisheries Investigations surveys. We focused on known murrelet prey, including larval Northern Anchovy *Engraulis mordax*, larval Pacific Saury *Cololabis saira*, larval rockfish *Sebastes* spp., and mesozooplankton (including euphausiids). We obtained data on upwelling and sea-surface temperature (SST) from the National Oceanic and Atmospheric Administration to characterize oceanographic conditions. Average clutch initiation date was earlier in years with abundant mesozooplankton, stronger upwelling, and lower SST. Average clutch size was higher in years with abundant larval saury and mesozooplankton and lower SST. These results suggest that murrelets in the Southern California Bight are influenced by “bottom-up” processes in which variability in oceanographic conditions affects breeding through effects on prey abundance.

Key words: Xantus's Murrelet, breeding biology, prey abundance, oceanographic conditions, Santa Barbara Island, Southern California Bight

INTRODUCTION

Many seabird studies have documented earlier breeding and higher reproductive success in years when prey is abundant (Cairns 1987, Croxall & Rothery 1991, Phillips *et al.* 1996). An increasing number of studies have focused on seabird responses to variability in oceanographic conditions (Ainley *et al.* 1995, Gaston & Smith 2001, Abraham & Sydeman 2004). Ocean productivity along the west coast of the United States is enhanced in the spring and summer by an influx of cool, nutrient-rich water from the north and localized upwelling that brings nutrients to the surface (Chelton *et al.* 1982, Schwing *et al.* 2000). Low sea-surface temperature (SST) and strong upwelling are, therefore, associated with high primary and secondary productivity in the region and can show substantial interannual variation (Chelton *et al.* 1982). Seabird studies have documented earlier breeding and higher reproductive success in years of stronger upwelling and lower SST, demonstrating the importance of “bottom-up” processes to higher trophic levels (Gaston & Smith 2001, Abraham & Sydeman 2004).

Relatively little is known about the effects of variability in prey abundance and oceanographic conditions on Xantus's Murrelet *Synthliboramphus hypoleucus* breeding. Early diet studies indicated that murrelets fed exclusively on larval fish, including larval Northern Anchovy *Engraulis mordax*, larval Pacific Saury *Cololabis saira*, and larval rockfish *Sebastes* spp. (Hunt *et al.* 1979). A more recent diet study indicated that murrelets feed on a wider variety of prey than previously thought, including subadult and adult anchovy, juvenile Bluefin Driftfish *Psenes pellucidus* or Medusafish *Ichthyos*

lockingtoni, and euphausiids *Thysanoessa spinifera* (Hamilton *et al.* 2004). The only previous study of the relationship between murrelet breeding and prey abundance focused on larval anchovy and found that murrelets delayed breeding when larval anchovies were unavailable until late in the season (Hunt & Butler 1980). However, larval anchovy abundance has declined since that study was conducted (Smith 1995). The effect of the decline on murrelet breeding is unknown. The effects of variation in other prey species abundances and oceanographic conditions on murrelet breeding are also unknown, though a study of the closely related Ancient Murrelet *Synthliboramphus antiquus* found that breeding success was higher in years of lower SST (Gaston & Smith 2001).

We used 19 years of data (1983–2001) to examine the influence of variability in prey abundance and oceanographic conditions on Xantus's Murrelet breeding. Our first objective was to evaluate the effect of variation in prey abundance on clutch initiation date, clutch size and hatching success. We focused on known murrelet prey, including larval anchovy, larval saury, larval rockfish, and mesozooplankton (including euphausiids). We expected that clutch initiation date would be earlier and clutch size and hatching success higher in years of higher prey abundance. Our second objective was to evaluate the effects of variation in upwelling and SST on clutch initiation date, clutch size and hatching success. We used Bakun's upwelling index (described in Schwing *et al.* 1996) and SST from a local buoy. We expected that clutch initiation date would be earlier and clutch size and hatching success higher in years of stronger upwelling and lower SST.

METHODS

Study area

Santa Barbara Island, California, USA (33°28'N, 119°02'W), part of Channel Islands National Park (CINP), is located within the Southern California Bight (SCB). The island supports the largest murrelet breeding population in the United States, including 1000–2500 birds (Burkett *et al.* 2003). The SCB extends along the coast from Point Conception, California, to Cabo Colonet, Baja California, Mexico (Daily *et al.* 1993; Fig. 1). The California Current flows in a southeasterly direction offshore of the Channel Islands and marks the western edge of the SCB. The California Current moves inshore just south of the border between California and Mexico. We selected the area between Point Conception and San Clemente Island as our study area because it encompasses the primary foraging range of murrelets associated with Santa Barbara Island (Fig. 1; Hunt *et al.* 1979, Whitworth *et al.* 2000).

Murrelet breeding

We used murrelet data from CINP's Seabird Monitoring Program. Seabird biologists checked individual nest sites in two study plots on Santa Barbara Island each year and recorded information on clutch initiation date, number of eggs laid and number of chicks hatched at each site. To minimize disturbance, they did not check sites every day or handle birds during visits to the sites. We used data from individual nest sites to calculate average clutch initiation date (Julian date) for first nesting attempts over 13 years during 1983–2001 (1983, 1985, 1986, 1989, 1992–1998, 2000/01). We were not able to include all years because nest monitoring started after the start of breeding in some years. We excluded years if more than 20% of nests were found on the first nest check of the season, and we excluded observations in all years if more than 14 days passed between surveys. The exclusions ensured that dates were within two weeks of actual clutch initiation dates. We calculated average clutch size and average hatching success (chicks hatched per egg laid) for first nesting attempts in each year from 1983 to

2001. We used hatching success as our measure of productivity, because chicks leave the nest site shortly after hatching and the remainder of the chick-rearing period occurs at sea (Murray *et al.* 1983, Drost & Lewis 1995).

Prey abundance

We used larval fish and zooplankton data from quarterly California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys (Paul Smith, National Marine Fisheries Service, pers. comm.). We used prey abundance data from Quarter 1 (January–March) to represent the prebreeding season and from Quarter 2 (April–June) to represent the breeding season (Table 1). We used data from a survey conducted in late March to represent Quarter 2 in 1983, and we excluded Quarter 2 in 1991 from our analyses because CalCOFI did not conduct any surveys during Quarter 2 in either of those years.

We used data from stations along Lines 80, 83, 87, and 90 (Fig. 1). Line 80 extends offshore from Point Conception; we used it to define the northern boundary of our presumed murrelet foraging ambit from Santa Barbara Island. Line 90 extends offshore north of San Clemente Island; we used it to define the southern boundary. We used data collected at stations inshore of Station 60 along all of the lines. This cutoff ensured that we were not including the offshore (blue water) domain in our analyses (Hayward & Venrick 1998). We excluded extra surveys conducted in some quarters, lines that were not sampled every year and stations that were sampled more than once during a single survey.

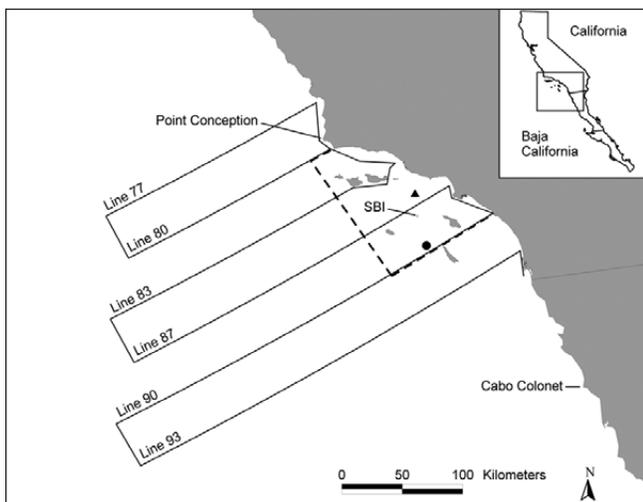


Fig. 1. Map showing the location of Santa Barbara Island (SBI), California, USA. The Southern California Bight extends from Point Conception, California to Cabo Colonet, Baja California, Mexico. The solid lines represent the California Cooperative Oceanic Fisheries Investigations transects. The dashed lines represent the boundaries of the study area. The triangle indicates the location of sea-surface temperature measurements. The circle indicates the location of upwelling index measurements.

TABLE 1
Dates of California Cooperative Oceanic Fisheries Investigations surveys for Quarters 1 and 2 from 1983–2001

Year	Quarter 1		Quarter 2	
	Date range	Stations sampled (n)	Date range	Stations sampled (n)
1983	2/9–3/6	17	3/22–3/28 ^a	17
1984	1/4–1/12	18	4/9–4/17	18
1985	2/25–3/1	18	5/6–5/16	18
1986	1/25–2/17	18	5/13–5/18	19
1987	3/7–3/13	17	5/5–5/11	19
1988	1/24–1/30	19	5/4–5/10	19
1989	1/25–1/31	19	4/21–4/28	19
1990	3/10–3/17	19	4/22–4/29	19
1991	1/13–1/19	19	No survey	N/A
1992	2/3–2/9	19	4/18–4/27	19
1993	1/17–1/23	19	4/4–4/11	19
1994	1/26–2/3	19	4/30–5/7	15
1995	1/10–1/17	18	4/11–4/18	19
1996	2/4–2/11	19	4/21–4/28	18
1997	2/3–2/10	19	4/7–4/15	16
1998	1/28–2/7	18	4/7–4/15	19
1999	1/14–1/22	18	4/6–4/13	19
2000	1/12–1/20	19	4/12–4/19	19
2001	1/13–1/20	19	4/11–4/20	19

^aLate March survey used to represent Quarter 2.

CalCOFI researchers collected larval fish and zooplankton at each station by towing paired Bongo nets with 505 μm mesh at a 45-degree angle from 210 m to the surface. Researchers identified and counted larval fish and standardized the data to $n/10 \text{ m}^2$ at each station. They measured zooplankton wet displacement volumes, and standardized the data to $\text{mL}/1000 \text{ m}^3$ strained. We used mesozooplankton data in our analyses. Mesozooplankton species are those with a wet displacement volume of less than 5 mL and include euphausiids. We averaged station data to obtain abundance estimates for each season in each year. We log transformed ($\log_{10} + 1$) individual station data before calculating averages to stabilize the variance (Zar 1999). We examined all species that are known murrelet prey and that are found in the CalCOFI dataset. Our final analyses included larval anchovy, larval saury, larval rockfish and mesozooplankton.

Upwelling and SST

We used Bakun's upwelling index (described in Schwing *et al.* 1996) and SST to characterize oceanographic conditions in the study area. We obtained monthly upwelling indices ($\text{m}^3 \times \text{s}^{-1} / 100 \text{ m}$ coastline) for the study area at 33°N, 119°W from the National Oceanic and Atmospheric Administration's (NOAA's) Pacific Fisheries Environmental Laboratory (Fig. 1; www.pfeg.noaa.gov). We averaged monthly values to obtain one value for each season in each year to match quarterly CalCOFI surveys. We obtained SSTs (degrees Celsius) for Station 46025 at 33°44'42"N, 119°05'02"W from NOAA's National Data Buoy Center (Fig. 1; www.ndbc.noaa.gov). The station is a 3-m discus buoy that measures water temperature at 0.6 m below sea level once every hour. We averaged hourly values to obtain one value for each season in each year to match quarterly CalCOFI surveys.

Statistical analyses

We used two-tailed Spearman rank correlations to evaluate the relationships between clutch initiation date, clutch size and hatching success, and each prey abundance or oceanographic variable for the prebreeding and breeding seasons (Zar 1999). We used rank correlations to establish the significance of relationships because

of the robustness of this technique. We report linear regression equations and r^2 values for significant relationships. We considered relationships significant at $P < 0.1$ because of the exploratory nature of these analyses. (See tables for more details on significance levels.) We conducted all analyses in Stata 8.0 (Stata Corporation 2003).

TABLE 2

Spearman rank correlation coefficients between average clutch initiation date, prey abundance and oceanographic conditions in the Southern California Bight during 1983–2001

Parameter	Prebreeding season	Breeding season
	(n=13 years)	(n=13 years)
Prey species		
Northern Anchovy	-0.25	0.32
Pacific Saury	0.00	-0.08
Rockfish spp.	-0.24	0.56 ^a
Mesozooplankton	-0.80 ^b	-0.51 ^c
Oceanographic conditions		
Upwelling	-0.55 ^a	-0.55 ^c
Sea-surface temperature	0.57 ^a	0.02

^a $P < 0.05$.

^b $P < 0.01$.

^c $P < 0.10$.

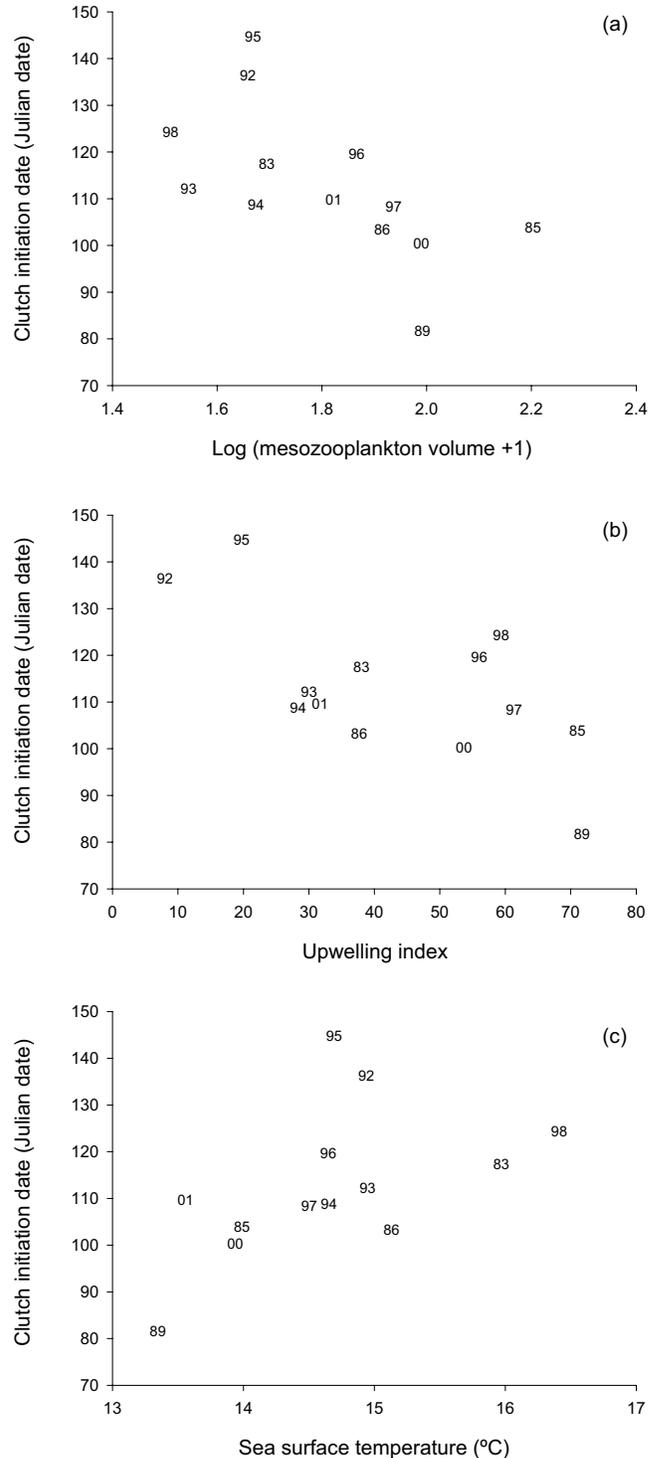


Fig. 2. Relationships between Xantus's Murrelet clutch initiation date and (a) mesozooplankton volume, (b) upwelling index and (c) sea-surface temperature during the prebreeding season over 1983–2001.

RESULTS

Clutch initiation date was negatively correlated with mesozooplankton volume and upwelling and positively correlated with SST during the prebreeding season [Table 2; Fig. 2(a-c)]. The corresponding regression equations were

$$y = 202.724 - 49.512 \times \log(\text{mesozooplankton volume} + 1) \quad (r^2 = 0.38),$$

$$y = 136.060 - 0.523 \times \text{upwelling index} \quad (r^2 = 0.42), \text{ and}$$

$$y = -30.774 + 9.797 \times \text{SST} \quad (r^2 = 0.28).$$

During the breeding season, clutch initiation date was negatively correlated with mesozooplankton volume and upwelling and positively correlated with larval rockfish abundance (Table 2). The corresponding regression equations were

$$y = 143.534 - 14.556 \times \log(\text{mesozooplankton volume} + 1) \quad (r^2 = 0.13),$$

$$y = 170.840 - 0.243 \times \text{upwelling index} \quad (r^2 = 0.34), \text{ and}$$

$$y = 108.831 + 4.011 \times \log(\text{larval rockfish abundance} + 1) \quad (r^2 = 0.02).$$

Clutch size was positively correlated with larval saury abundance and mesozooplankton volume and negatively correlated with SST during the prebreeding season [Table 3; Fig. 3(a-c)]. The relationship between clutch size and larval saury abundance was dependent on two (1999 and 2001) of the 19 years. The corresponding regression equations were

$$y = 1.548 + 2.652 \times \log(\text{larval saury abundance} + 1) \quad (r^2 = 0.31),$$

$$y = 1.195 + 0.201 \times \log(\text{mesozooplankton volume} + 1) \quad (r^2 = 0.14), \text{ and}$$

$$y = 2.382 - 0.055 \times \text{SST} \quad (r^2 = 0.16).$$

During the breeding season, clutch size was positively correlated with mesozooplankton volume and negatively correlated with SST (Table 3). The corresponding regression equations were

$$y = 1.361 + 0.096 \times \log(\text{mesozooplankton volume} + 1) \quad (r^2 = 0.08) \text{ and}$$

$$y = 2.579 - 0.061 \times \text{SST} \quad (r^2 = 0.18).$$

TABLE 3

Spearman rank correlation coefficients between average clutch size, prey abundance and oceanographic conditions in the Southern California Bight during 1983–2001

Parameter	Prebreeding season	Breeding season
	(n=19 years)	(n=18 years)
Prey species		
Northern Anchovy	-0.19	-0.39
Pacific Saury	0.47 ^a	0.18
Rockfish spp.	-0.12	0.22
Mesozooplankton	0.43 ^b	0.42 ^b
Oceanographic conditions		
Upwelling	0.24	0.01
Sea-surface temperature	-0.46 ^a	-0.41 ^b

^a $P < 0.05$.

^b $P < 0.10$.

There were no significant relationships between hatching success and prey abundance or oceanographic variables during either the prebreeding or breeding seasons (Table 4).

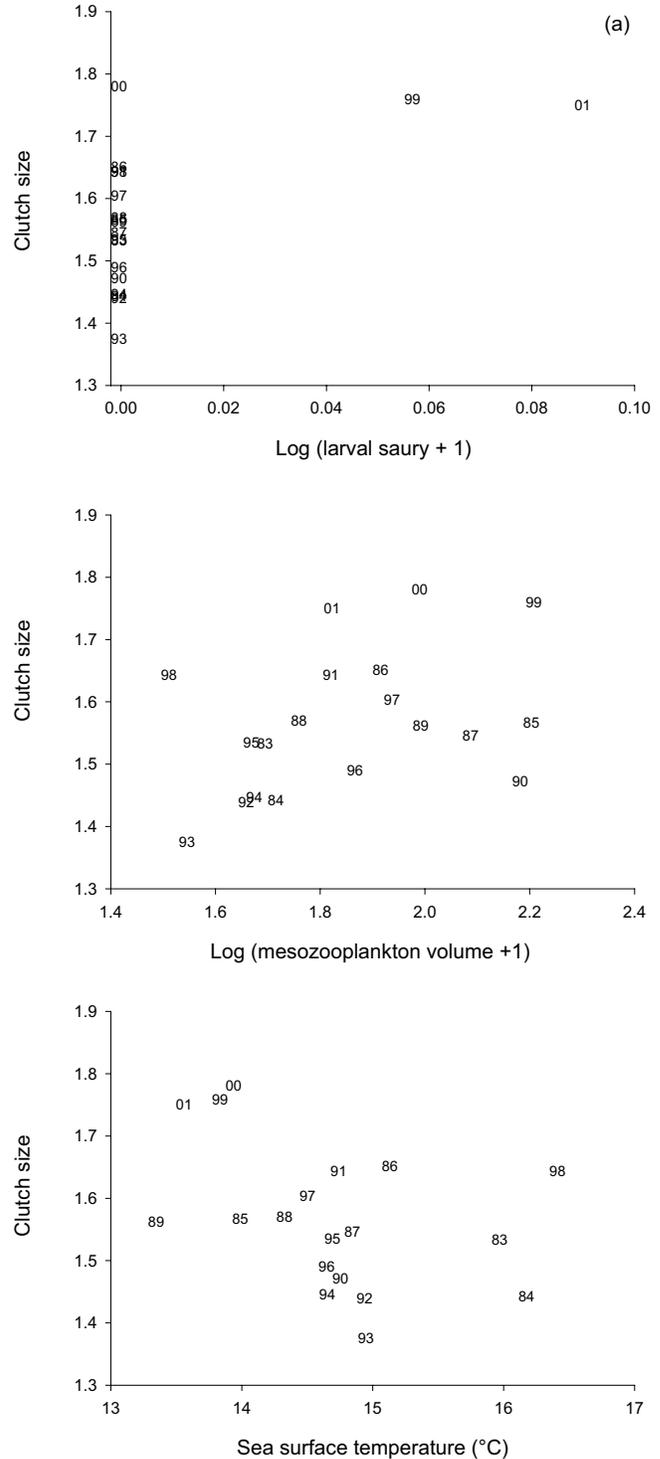


Fig. 3. Relationships between Xantus's Murrelet clutch size and (a) larval saury abundance, (b) mesozooplankton volume and (c) sea-surface temperature during the prebreeding season over 1983–2001.

DISCUSSION

Predator–prey relationships

Average clutch initiation date was earlier in years with abundant mesozooplankton. In addition, average clutch size was higher in years with abundant larval saury and mesozooplankton. We did not find the relationship between clutch initiation date and larval anchovy abundance documented by Hunt & Butler (1980), but our results support their more general conclusion that timing of breeding is influenced by prey abundance. Our results are also consistent with other seabird studies that have documented earlier breeding and increases in breeding parameters (e.g. clutch size, hatching success, productivity) in response to abundant prey (Anderson *et al.* 1982, Schaffner 1986, Monaghan *et al.* 1989, Sydeman *et al.* 1991, Crawford & Dyer 1995, Phillips *et al.* 1996, Suddaby & Ratcliffe 1997, Ratcliffe *et al.* 1998, Nur & Sydeman 1999, Abraham & Sydeman 2004). Larval saury and mesozooplankton (euphausiids) are known murrelet prey species (Hunt *et al.* 1979, Hamilton *et al.* 2004), and our results may indicate that they are specifically important in determining murrelet timing of breeding and clutch size. Alternatively, larval saury and mesozooplankton may be proxies for general prey abundance. The results were similar between the prebreeding and breeding seasons, with the exception of a positive relationship between clutch initiation date and larval rockfish abundance during the breeding season. That relationship does not appear to have any biological relevance and is likely a spurious correlation.

Hunt & Butler (1980) found a relationship between timing of breeding and larval anchovy abundance and concluded that larval anchovies were of particular importance to murrelets. We did not find a relationship between these variables in our time series. A decline in larval anchovy numbers may be responsible for the difference between the two studies. Larval anchovy abundance peaked in the mid-to-late 1970s (Ahlstrom 1966, MacCall & Prager 1988), when Hunt & Butler (1980) conducted their study. Anchovy abundance declined during the 1980s and 1990s (Smith 1995) and may be a less prevalent diet item than in the past. The lack of a relationship between murrelet breeding and larval anchovy abundance, significant relationships between murrelet breeding and other measures of prey abundance, and evidence that murrelets are generalists (Hamilton *et al.* 2004) suggest that murrelets exploit a

variety of prey species depending on their relative abundances in the environment. Studies of the closely related Ancient Murrelet also support this idea. Ancient Murrelets are generalists (Sealy 1975, Vermeer *et al.* 1985, Gaston *et al.* 1993, Gaston 1994), whose diet composition varies both seasonally and geographically depending on prey abundances (Sealy 1975, Vermeer *et al.* 1985).

Hatching success was not related to prey abundance. The lack of a relationship is likely attributable to the influence of egg predation on hatching success. Sydeman *et al.* (1998) found that approximately 47% of the eggs were preyed upon by native deer mice on Santa Barbara Island from 1983 to 1995. However, it is important to note that prey abundance may have an indirect effect on egg predation. Egg neglect appears to increase in years of low prey abundance (Murray *et al.* 1979). Sydeman *et al.* (1998, 2001) suggested that there may be an interaction between prey abundance and mouse predation that determines hatching success. In that case, increased egg neglect in years of low prey abundance would lead to higher predation and lower hatching success. Blight *et al.* (1999) proposed a similar mechanism for Rhinoceros Auklets *Cerorhinca monocerata* subjected to egg predation by native deer mice.

Predator–oceanographic relationships

Average clutch initiation dates were earlier in years with stronger upwelling and lower SST. In addition, average clutch sizes were higher in years with lower SST. These results, coupled with results of predator–prey interactions, offer evidence for the influence of “bottom-up” processes on murrelet breeding. Annual productivity in the SCB is influenced by the strength of the California Current and seasonal upwelling. The California Current brings cool, nutrient-rich waters into the region from the north (Chelton *et al.* 1982, Daily *et al.* 1993). Coastal upwelling near Point Conception and localized upwelling near headlands and islands replaces surface waters with cool, nutrient-rich waters from below (Daily *et al.* 1993, Schwing *et al.* 2000). The increase in nutrients at the surface leads to increases in primary and secondary (fish and zooplankton) productivity (Chelton *et al.* 1982, Schwing *et al.* 2000) that are beneficial for seabirds. Our results are consistent with seabird studies from other areas that have documented relationships between breeding parameters and oceanographic conditions. For instance, Gaston & Smith (2001) found that Ancient Murrelet breeding success was higher in years with lower SST. In addition, Abraham & Sydeman (2004) found that Cassin's Auklet *Ptychoramphus aleuticus* hatching dates were earlier in years with lower SST and stronger upwelling.

Given the association between murrelets and oceanographic conditions, recent changes in the SCB may have long-term implications for murrelets. The SCB was characterized by relatively warm SST and low productivity between the late 1970s and the late 1990s (McGowan *et al.* 2003), and murrelet reproductive success declined concordantly from 1985 to 1997 (Sydeman *et al.* 2001). In late 1998, there was a rapid shift to lower SST and higher productivity throughout the region (Bograd *et al.* 2000, Schwing *et al.* 2000). This may have marked a shift to a new “regime,” characterized by cooler, more productive conditions (Bograd *et al.* 2000, Schwing *et al.* 2000, Peterson & Schwing 2003).

We do not yet have enough data to quantitatively compare the two “regimes” or to assess murrelet responses to the shift. However, earlier breeding and increased clutch size and hatching success after 1999 suggest that murrelets are responding positively to this

TABLE 4
Spearman rank correlation coefficients between average hatching success, prey abundance and oceanographic conditions in the Southern California Bight during 1983–2001

Parameter	Prebreeding season	Breeding season
	(n=19 years)	(n=18 years)
Prey species		
Northern Anchovy	-0.23	-0.17
Pacific Saury	0.26	0.33
Rockfish spp.	0.03	0.13
Mesozooplankton	0.12	0.33
Oceanographic conditions		
Upwelling	-0.24	-0.39
Sea-surface temperature	-0.36	-0.37

ecosystem shift. Several seabird species—including Cassin's Auklet, Pelagic Cormorant *Phalacrocorax pelagicus*, and Pigeon Guillemot *Cepphus columba*—breeding off Central California showed similar increases in reproductive success after 1998 (Schwing *et al.* 2002). The California Current System appears to alternate between warm and cool regimes on multidecadal scales (Chavez *et al.* 2003), and the recent shift to a cooler, more productive ecosystem may have a positive effect on the murrelet population if it persists.

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BREEDING BIOLOGY OF XANTUS'S MURRELET AT THE SAN BENITO ISLANDS, BAJA CALIFORNIA, MÉXICO

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SUMMARY

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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 ± 0.78 and 1.11 ± 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 5000–10 000 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.*

(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

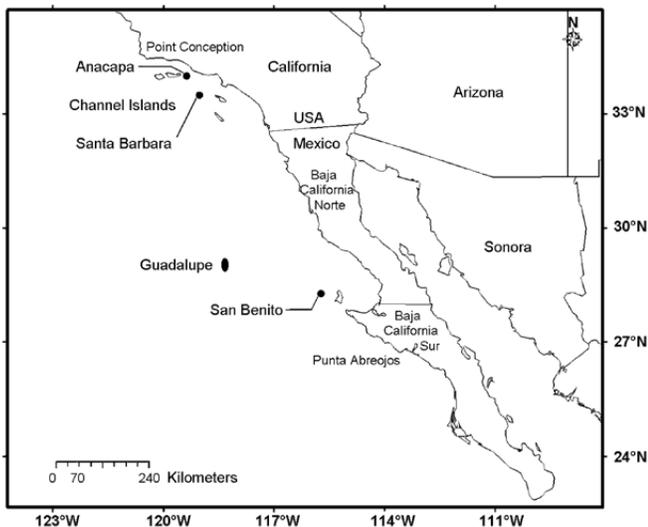


Fig. 1. Breeding range of Xantus's Murrelets from Point Conception, California, to Punta Abreojos, Baja California Sur, showing locations of Santa Barbara, San Benito, Anacapa and Guadalupe islands.

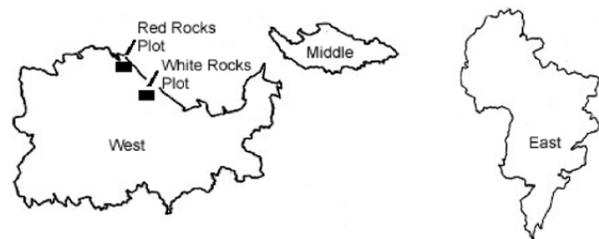


Fig. 2. Location of Red Rocks and White Rocks study plots on West San Benito Island. (Map reproduced with permission from Pronatura Noroeste [1998].)

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

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 (\bar{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 (\bar{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), 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.

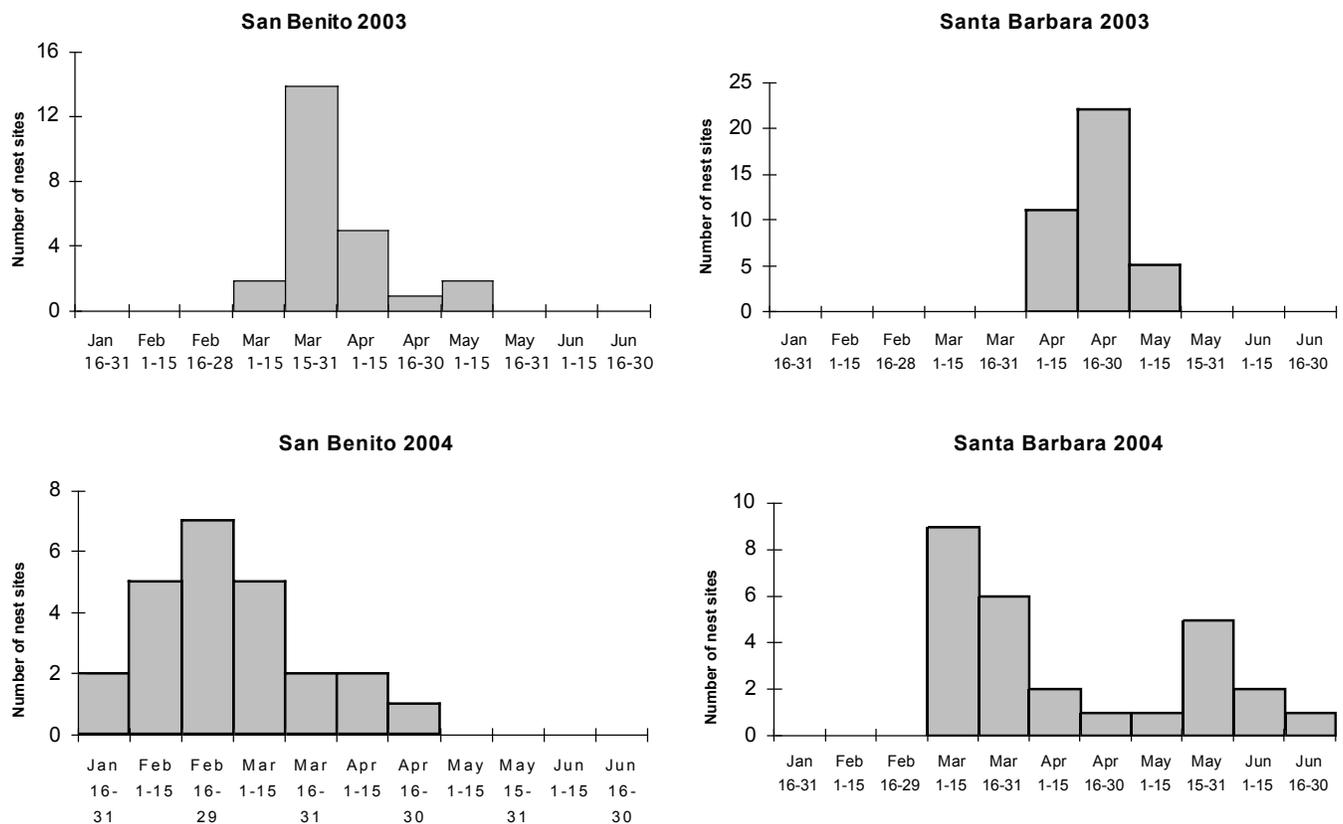


Fig. 3. Timing of clutch initiation on West San Benito Island and Santa Barbara Island in 2003 and 2004.

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 \times 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 \times one subspecies pairs, and 100% (1/1) for the mixed *scrippsi* \times *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 (\bar{X} = 19 April) in 2003 (n = 38) and 5 March to 21 June (\bar{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

both 2003 (χ^2 = 16.36, df = 1, P < 0.001) and 2004 (χ^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 (χ^2 = 18.03, df = 1, P < 0.001) in 2003, but not in 2004 (χ^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,

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

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.

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INITIAL RECOVERY OF XANTUS'S MURRELETS FOLLOWING RAT ERADICATION ON ANACAPA ISLAND, CALIFORNIA

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SUMMARY

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.

At Anacapa Island, California, breeding effort, hatching success and nesting distribution of Xantus's Murrelets *Synthliboramphus hypoleucus* increased in the years following the eradication of Black Rats *Rattus rattus* (2003–2005) as compared with pre-eradication years (2000–2002). Within sea-cave study areas, nest-site occupancy increased from 36% to 51%, nesting attempts increased 42%, hatching success increased from 42% to 80% and nest depredation decreased from 52% (by rats) to 7% (by endemic Deer Mice *Peromyscus maniculatus anacapae*). Post-eradication, murrelets and Cassin's Auklets *Ptychoramphus aleuticus* began nesting in habitats previously occupied by rats, including Cat Rock, where murrelet breeding was last reported in 1927. Initial post-eradication signs of recovery of Xantus's Murrelets at Anacapa Island are encouraging for eventual restoration of this important colony, but additional monitoring is needed to better document the rate and process of recovery.

Key words: Anacapa Island, Black Rat, breeding, eradication, introduced predator, *Rattus rattus*, recovery, restoration, *Synthliboramphus hypoleucus*, Xantus's Murrelet

INTRODUCTION

The catastrophic effects that introduced mammals have wrought on island-breeding seabirds are well known, often resulting in great population reductions or local extinctions (Moors & Atkinson 1984, Bailey & Kaiser 1993, Burger & Gochfeld 1994). In the 19th and 20th centuries, nonnative mammalian predators, especially cats *Felis catus* and rats *Rattus* spp., were introduced on many coastal islands used for breeding by Xantus's Murrelets *Synthliboramphus hypoleucus* in southern California and northwestern Baja California, causing reductions in murrelet population sizes, restricted distributions and possible extirpations (Jehl & Bond 1975, Jehl 1984, Drost & Lewis 1995, McChesney & Tershy 1998, Keitt 2005). At Anacapa Island, California, the severe impact on the murrelet population of nonnative Black Rats *Rattus rattus* has been recorded since at least early in the 20th century (Collins 1979, Hunt *et al.* 1979, Carter *et al.* 1992, McChesney & Tershy 1998, McChesney *et al.* 2000, Whitworth *et al.* 2003a). Anacapa Island harbors abundant potential nesting habitat, but only a remnant murrelet population persisted in the 1990s by nesting in habitats such as sea caves, steep slopes and cliffs, although evidence of rats and rat-depredated murrelet nests were found even in those relatively inaccessible habitats (McChesney *et al.* 2000; Whitworth *et al.* 2003a; H. Carter, unpubl. data).

With 1998 litigation settlement funds related to the 1990 *American Trader* oil spill, the American Trader Trustee Council (ATTC) sponsored a seabird restoration program on Anacapa Island by eradicating Black Rats (ATTC 2001). Island Conservation and the

National Park Service eradicated rats from Anacapa Island using helicopter-broadcast poison pellets on East Anacapa in December 2001 and Middle and West Anacapa in November 2002 (Howald *et al.* 2005). Breeding seabirds were expected to greatly benefit from rat eradication at Anacapa Island, but adequate baseline data did not exist for population size, breeding distribution or breeding success for nocturnal crevice-nesting species before the introduction of rats. Previous eradication programs had eliminated introduced predators on several murrelet breeding islands since about 1970 without quantifying the degree and rate of murrelet recovery (Hunt *et al.* 1979, McChesney & Tershy 1998). At Anacapa Island, the Xantus's Murrelet population was expected to benefit from rat eradication because the potential extirpation of this small remnant colony could be prevented and much suitable nesting habitat would be available for restoration of a relatively large colony (McChesney *et al.* 2000).

During 2000–2003, a monitoring team (Humboldt State University, California Institute of Environmental Studies, Channel Islands National Marine Sanctuary, and Hamer Environmental) gathered pre-eradication and first year post-eradication baseline data on murrelet population size, distribution and breeding success at Anacapa, using spotlight surveys and nest monitoring over the entire island (Whitworth *et al.* 2003a) and radar surveys over a portion of Middle Anacapa (Hamer *et al.* 2003, 2005). With reduced funding in 2004/05, the California Institute of Environmental Studies and Channel Islands National Marine Sanctuary continued sea-cave nest monitoring and nest searches in other sample areas (begun in 2003) to provide cost-effective annual information on the progress of

recovery after eradication. In this paper, we summarize the results of nest monitoring at Anacapa Island during 2000–2005, compare breeding indices pre- and post-eradication, and discuss initial signs of recovery of the Anacapa murrelet colony. Greater detail on methods and results is available in annual reports (Whitworth *et al.* 2002a, 2002b, 2003a, 2003b, 2004, 2005).

METHODS

Study area

Anacapa Island, the easternmost and smallest of the northern four California Channel islands, lies 15 km southwest of Ventura, California. It comprises three small islets (West, Middle and East Anacapa; Fig. 1) separated by narrow channels forming a chain approximately 7.5 km long with 17.5 km of coastline composed of steep, rocky cliffs indented with more than 100 sea caves (Bunnell 1993). West Anacapa is the largest (1.7 km²) and highest (284 m) of the three islets, followed by Middle Anacapa (0.6 km², 99 m) and East Anacapa (0.5 km², 73 m). Anacapa Island is managed by Channel Islands National Park, which maintains quarters for staff and facilities for campers on East Anacapa, but otherwise the island is uninhabited.

Nest monitoring

During 2000–2005, we searched for and monitored nests in 10 sea caves on Middle and West Anacapa (Fig. 1) where evidence of murrelet nesting had been observed in 1994–1997 (McChesney *et al.* 2000; H. Carter, unpubl. data). These caves included Refuge, Lava Bench #1, Lava Bench #2, Respiring Chimney, Lonely at the Top, Confusion, Pinnacle, Moss, Aerie and Keyhole (names after Bunnell 1993). We monitored nests every one to three weeks in April–July 2000, weekly in March–June 2001–2004 and biweekly in April–June 2005. All potential nesting habitat in sea caves was searched using hand-held flashlights during each visit. Access to sea caves and other sample areas involved drop-off and pick-up with a 3.8-m inflatable craft.

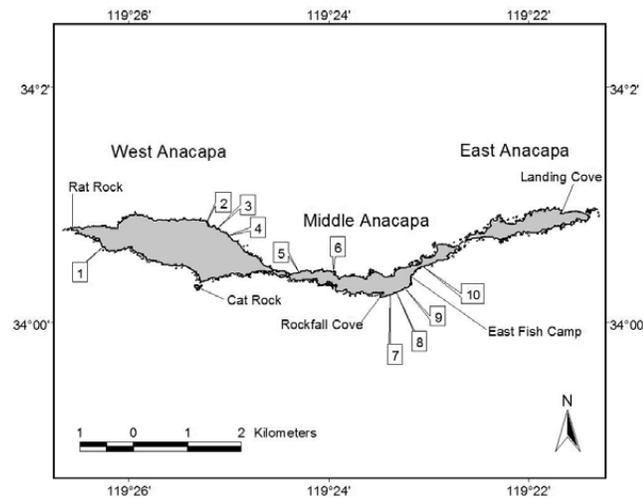


Fig. 1. Locations of 10 sea caves and other areas at Anacapa Island, California, where Xantus's Murrelet nest sites were monitored during 2000–2005. (1) Lonely at the Top; (2) Confusion; (3) Pinnacle; (4) Moss; (5) The Aerie; (6) Keyhole; (7) Respiring Chimney; (8) Lava Bench #2; (9) Lava Bench #1; and (10) Refuge. Other monitored areas are named, and larger coastal sections also are outlined in black.

Monitored sites were identified as suitable crevices or sheltered sites with evidence of current or past use as a nest (i.e. incubating or brooding adult, intact unattended eggs, broken or hatched eggshell fragments, or eggshell membranes). Site locations were marked with small numbered metal tags. We recorded the contents of each monitored site and any newly discovered nests during each visit. To prevent nest abandonment, incubating adults were observed briefly with a flashlight and occasionally photographed, but were not handled or prodded.

Systematic efforts to examine potential murrelet nesting areas in cliff, shoreline and offshore rock habitats began in 2003 and were expanded in 2004/05. We used methods similar to sea-cave nest monitoring to thoroughly search

- cliffs in Landing Cove on East Anacapa (2003–2005),
- Cat Rock (offshore rock) and Rat Rock (rocky peninsula) off West Anacapa (2003–2005),
- shoreline area of East Fish Camp on the south side of Middle Anacapa (2004–2005), and
- Rockfall Cove on the south side of Middle Anacapa (2005).

All previously tagged nests in those sample areas were checked during each visit, but more extensive nest searches were conducted only once or twice during the breeding season after egg laying had commenced in the sea caves.

Annual hatching success was determined as the percentage of active nests where at least one egg hatched, as determined by the presence of chicks or hatched eggshell fragments (dried or bloody membrane separated from the shell) found in or near the nest site. Nests that failed to hatch were classified as depredated (broken eggshells in or near the site, or eggs missing and presumed removed by rats or mice before hatching) or abandoned (intact unattended eggs over two consecutive checks). Rat-depredated eggs had larger bite marks on shell edges or crushing of eggshells; mouse-depredated eggs had smaller bite marks on shell edges with little or no crushing. Once nest fate had been determined, we removed any abandoned, broken or hatched eggshells to avoid confusion between previous and future nesting efforts.

Annual nest occupancy was the percentage of all monitored sites found between 2000 and 2005 in which nesting attempts occurred in a given year. All sea caves were searched thoroughly during each visit; therefore, we believe that untagged potential sites were unoccupied before the first evidence of nesting was observed and the nest was tagged. Using this method, the occupancy calculated for past years will decrease as new sites are added in future years, until all potential nest sites in each cave have been occupied. Determining occupancy rates in this way will best reflect growth of the murrelet population. Estimates of occupancy in sample areas outside the sea caves were calculated similarly, but because systematic nest searches began in different years (as described earlier), the total number of monitored sites used to calculate occupancy differed among years.

Timing of breeding was estimated using murrelet breeding biology data from Murray *et al.* (1983) to determine the midpoint of the range of possible clutch initiation dates for each active nest and at-sea observation of chicks accompanied by adults as they left the island. For statistical comparison of murrelet performance pre- and post-eradication of rats, we used *G*-tests, including the Yates correction (G_c) for 2×2 tables (Zar 1999).

RESULTS

Nest monitoring in sea caves

During 2000–2005, we recorded 28 murrelet nest sites in nine caves on Middle and West Anacapa Island (Table 1), but found none in Confusion Cave. In 2000, we monitored 13 nest sites, including nine occupied sites and four non-occupied old sites. Only three new sites (+23%) were added from 2000 to 2002, compared with 12 new sites (+75%) since 2002. We recorded eight new sites in 2003, the first breeding season after rat eradication on Middle and West Anacapa. From 2000 to 2005, 75 nesting attempts were initiated, with increasing numbers each year except 2004, when overall murrelet breeding was delayed and much reduced. The number of nests initiated increased 42% after eradication. Annual nest occupancy ranged from 32% to 61% (Table 1) and increased from 36% pre-eradication to 51% post-eradication, although the increase was not significant ($G_c = 3.50$, $df = 1$, $P > 0.05$).

Differences in the frequencies of nest fates were observed in the post- and pre-eradication periods ($G = 20.06$, $df = 2$, $P < 0.001$). Overall hatching success was 64%, but was much higher ($G_c = 9.65$, $df = 1$, $P < 0.005$) post-eradication (80%) than pre-eradication (42%). Post-eradication hatching success was consistently high (73%–83%; Table 1, Fig. 2); pre-eradication, it was quite variable (18%–78%). However, high hatching success in 2000 did not take into account rat-depredated eggs of unknown origin (i.e. eggs removed from monitored sites before nesting was detected or from non-monitored nest sites in a few inaccessible deep crevices) found in several caves in 2000/01.

During 2000–2005, the nest failure rate was 36%, with 19 depredated nests (25%) and eight abandoned nests (11%). Abandonment was similar ($G_c = 0.39$, $df = 1$, $P > 0.25$) pre- and post-eradication (14% and 6% respectively), but depredation was much lower ($G_c = 17.49$, $df = 1$, $P < 0.001$) post-eradication (7%) than pre-eradication (52%; Table 1, Fig. 2). Highest depredation rates were recorded pre-eradication in 2001 and 2002. No depredated nests were noted in 2005, although a missing egg in 2003 and two depredated nests in 2004 were attributed to endemic Deer Mice *Peromyscus maniculatus*

anacapae. Two depredated adult murrelets were found in sea caves. One partly eaten carcass, likely killed by a rat, was found inside a monitored site in March 2001 before egg laying. In the second instance, raptor-depredated plucked murrelet feathers and mouse-depredated eggs were found outside an active site in 2004.

Colony expansion

During 2003–2005, 12 nesting attempts in 10 sites were discovered in cliffs, shoreline or offshore rocks where none had been found during sporadic nest searches since 1991 (Table 2). Occupied murrelet nest sites were first found in the Landing Cove cliffs (one site) and Cat Rock (one site) in 2003. Two more occupied nest sites were discovered in 2004, one in Landing Cove and another along the shoreline of East Fish Camp. The latter site was destroyed by a landslide during storms in the winter of 2004/05. Six new occupied sites were found in 2005, four in Landing Cove and two in Rockfall Cove. Occupancy in monitored nest sites outside sea caves was low in 2003 (29%) and 2004 (25%), but increased to 89% in 2005. Nearly all (92%) of these nesting attempts successfully hatched, with only one abandoned and no depredated nests.

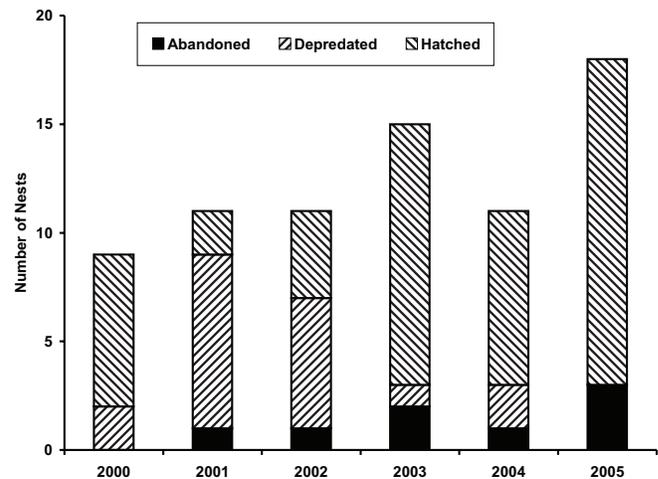


Fig. 2. Number of abandoned, depredated and hatched Xantus's Murrelet nests in sea caves at Anacapa Island, California, 2000–2005.

TABLE 1
Breeding effort and success of Xantus's Murrelets in sea caves at Anacapa Island during 2000–2005

Nest site summary	Pre-eradication year				Post-eradication year			
	2000	2001	2002	2000–2002	2003	2004	2005	2003–2005
Tagged & monitored	13	15	16	16	24	25	28	28
Potential	28	28	28	28	28	28	28	28
Nesting attempts	9	11	11 ^a	31	15	11	18 ^a	44
Occupied	9	11	10 ^a	—	15	11	17 ^a	—
(occupied/potential)	32%	39%	36%	36%	54%	39%	61%	51%
Hatched	7	2	4	13	12	8	15	35
(hatched/nesting attempts)	78%	18%	36%	42%	80%	73%	83%	80%
Depredated	2	8	6	16	1	2	0	3
(depredated/nesting attempts)	22%	73%	55%	52%	7%	18%	0%	7%
Abandoned	0	1	1	2	2	1	3	6
(abandoned/nesting attempts)	0%	9%	9%	6%	13%	9%	17%	14%

^a Two nesting attempts in one site treated as separate nesting attempts.

Timing of breeding

Murrelet nests were initiated between 3 March and 3 June during 2000–2005. Mean annual clutch initiation dates ranged from 30 March (± 11 days) in 2000 to 2 May (± 14 days) in 2005. Assuming little error in using midpoints to estimate the date of clutch initiations, timing of breeding differed significantly from year to year (ANOVA $F_{5,87} = 12.41$, $P < 0.0001$), with later initiation in 2004 and 2005 than in 2000–2003 (Tukey HSD test; all $P < 0.03$).

Other nesting seabirds

Two Cassin's Auklet *Ptychoramphus aleuticus* nests were discovered on Rat Rock in 2003, and both fledged chicks. Only one of these auklet nests was occupied in 2004, but the egg was soon abandoned. Egg laying occurred in both nest sites in 2005, but breeding success could not be determined because of concern for potential disturbance to nearby breeding Brandt's Cormorants *Phalacrocorax penicillatus*. Eight Pigeon Guillemot *Cephus columba* nests were discovered in two sea caves during 2003–2005, but breeding success could not be determined. Two guillemot nest sites occupied annually since 2003 were located in sites formerly used by murrelets; in one case, an occupied murrelet nest was usurped by guillemots.

DISCUSSION

Nesting effort and breeding success of Xantus's Murrelets at Anacapa Island have improved after the eradication of Black Rats from the island in 2002. The number of monitored nests sites increased 75%, the number of nesting attempts increased 42%, occupancy increased from 36% to 51%, hatching success increased from 42% to 80% and nest depredation decreased from 52% to 7%. In addition, nesting distribution increased, with 10 nest sites discovered in sample areas outside of sea caves during 2003–2005, where none had been found since 1991. With this initial response to rat eradication, we are confident that rat predation has been the primary negative impact on the Anacapa murrelet colony over the past century, although serious impacts from the 1969 Santa Barbara

oil spill also likely occurred (McChesney & Tershey 1998, Carter *et al.* 2000, McChesney *et al.* 2000).

Nest searches and monitoring were limited to 10 sea caves during 2000–2002, because these were the only accessible areas for monitoring with recent known nesting. Fortunately, we found sufficient nest sites for monitoring in these caves to obtain a comparable baseline for describing murrelet breeding conditions pre-eradication. Standardized comparisons of breeding effort and success within sea caves effectively demonstrated initial improvements in murrelet breeding conditions for three years post-eradication. However, available habitat for new nests is limited in these caves and may be saturated soon, allowing future measurement of breeding success only.

With limited funding after 2003, we used nest searches in sample areas to augment cave monitoring and to detect when murrelets began colonizing nesting areas where prior breeding was prevented by rats. Occasional nest searches during 1991–2002 failed to find any nests at Landing Cove cliffs and Cat Rock, although single depredated nests were found at Landing Cove cliffs in 1987 and 1988, and fragments of depredated eggs were found on West Anacapa in 1991 and 1997 (Carter *et al.* 1992; McChesney *et al.* 2000; Whitworth *et al.* 2003a; H. Carter, unpubl. data). We suspect that few nests were initiated in sample areas before 2003, but once nests become more abundant, monitoring should be shifted to these and other accessible areas to further document colony growth. Rapid colony expansion into suitable but previously unoccupied nesting habitats on Anacapa Island (particularly the cliffs in Landing Cove) is encouraging for rapid colony growth to much higher population levels. Sufficient nesting habitat exists at Anacapa Island to support thousands of breeding pairs (McChesney *et al.* 2000), and indeed murrelets were once considered common breeding birds on Anacapa (Howell 1917). Museum specimens collected in the early 20th century revealed that murrelets once nested much more widely at East and West Anacapa and Cat Rock (McChesney *et al.* 2000; H. Carter, unpubl. data).

Post-eradication breeding by Cassin's Auklets on Rat Rock further illustrated the benefits of rat eradication for nocturnal crevice-nesting seabirds. Auklets probably nested on Anacapa in the early 1900s (Willett 1910), but the only direct evidence of breeding pre-eradication was one depredated egg found in a sea cave in 1997 (McChesney *et al.* 2000). Pigeon Guillemots have long nested at Anacapa Island (Hunt *et al.* 1979, Carter *et al.* 1992), but monitoring suggests that their numbers and distribution also may expand post-eradication. Wider habitat searches and use of other monitoring techniques such as mist-netting will be needed to detect establishment and growth of other seabird colonies, including Ashy Storm-Petrels *Oceanodroma homochroa*, which may already nest in small numbers on Anacapa Island (Carter *et al.*, in press). To prevent disturbance to other sensitive seabird species, nest searches in upper habitats at West Anacapa will need to be conducted in the fall, after Brown Pelicans *Pelecanus occidentalis* and Double-crested Cormorants *Phalacrocorax auritus* have finished breeding (McChesney *et al.* 2000).

Detectable increases in the overall Anacapa murrelet population were not expected for several years, because murrelets, like all alcids, have relatively low reproductive rates, strong natal philopatry and deferred sexual maturity (Murray *et al.* 1983, Drost & Lewis 1995, Gaston & Jones 1998). The congeneric Ancient Murrelet *S. antiquus* colony on Langara Island in British Columbia appears to be slowly recovering

TABLE 2

Breeding effort and success of Xantus's Murrelets in sample areas outside of sea caves at Anacapa Island, 2003–2005

Nest site summary	2003	2004	2005	2003–2005
Tagged & monitored	2	4	9 ^a	9 ^a
Potential	7	8	9 ^a	9 ^a
Nesting attempts	2	2	8	12
Occupied	2	2	8	—
(occupied/potential)	29%	25%	89%	50%
Hatched	2	1	8	11
(hatched/nesting attempts)	100%	50%	100%	92%
Depredated	0	0	0	0
(depredated/nesting attempts)	0%	0%	0%	0%
Abandoned	0	1	0	1
(abandoned/nesting attempts)	0%	50%	0%	11%

^a Excludes one tagged site destroyed by a landslide (see text).

following the eradication of introduced Norway Rats *R. norvegicus* in 1995. A halt in the population decline at the colony had been noted by 1999 (Drever 2002). By 2004, increases in breeding population size, colony area and burrow occupancy—plus the establishment of a small Cassin's Auklet colony—emphasized the improvement in breeding conditions for seabirds on Langara since the removal of rats (Regehr *et al.*, in press).

High hatching success and increased nesting effort by murrelets at Anacapa from 2003 to 2005 should contribute to strong recruitment in 2006 and beyond. By 2005, a relatively strong cohort of first-time breeders (probably 2–4 years, as in the Ancient Murrelet; Gaston 1990) may have recruited into the population following the first phase of rat-eradication on East Anacapa in 2001. However, some colony growth and expansion had begun by 2003, suggesting that subadults or nonbreeding adults already present in at-sea congregations (Whitworth *et al.* 1997, 2000) probably assisted early growth and expansion. We anticipate increased breeding effort and colony expansion in the near future, but factors unrelated to rat predation also could affect murrelet breeding.

Nesting effort and breeding success of murrelets in the Southern California Bight can vary dramatically between years and even between decades because of high variability in the availability of prey resources (Hunt & Butler 1980; Drost & Lewis 1995; Whitworth *et al.* 2000; Hamilton *et al.* 2004, 2005; Roth *et al.* 2005). Fewer nesting attempts in 2004 and delayed breeding in 2004/05 at Anacapa Island likely reflected delayed prey availability in the Bight, although hatching success was not greatly affected. Survival to breeding age in alcids may also be affected by various natural and anthropogenic factors (Hudson 1985). Murrelets are extremely vulnerable to oil spills or light pollution near colonies (Carter *et al.* 2000, Burkett *et al.* 2003), which could hinder colony recovery.

Possible future impacts of endemic Deer Mice on Xantus's Murrelets at Anacapa Island are difficult to predict. Wild Deer Mice were eliminated during the rat eradication, although a captive population was retained and released one year afterward. Mice quickly repopulated the island, although numbers in shoreline habitats did not reach higher levels until about one year after release (Howald *et al.* 2005; H. Gellerman & G. Howald, pers. comm.). Before eradication, mice on Anacapa were greatly reduced by rats, especially in shoreline habitats, and had little or no effect on murrelet nesting in sea caves. At present, Anacapa murrelets have higher hatching success and lower depredation rates than at Santa Barbara Island, where cyclically high mouse and owl densities in human-altered grassland habitats near murrelet breeding areas have led to high depredation rates (Murray *et al.* 1983, Drost & Lewis 1995, Schwemm & Martin 2005, Wolf *et al.* 2005). However, mice preyed upon small numbers of murrelet nests in 2004/05 and may have greater effects in the future.

Continued annual nest monitoring is needed to document expected colony growth, given initial signs of colony expansion. To identify and quantify overall changes in population size and distribution, spotlight surveys (which count birds at night on transects within at-sea congregations off East, Middle and West Anacapa) and radar surveys at Middle Anacapa should be conducted for comparison to pre-eradication surveys (Whitworth *et al.* 2003a; Hamer *et al.* 2003, 2005). Considering rapid changes during 2003–2005, changes in total population size and distribution should be examined in the near future.

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RADAR AS A TOOL FOR MONITORING XANTUS'S MURRELET POPULATIONS

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SUMMARY

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Xantus's Murrelets *Synthliboramphus hypoleucus* are vulnerable to extirpation from breeding islands because of high mortality rates from introduced mammalian predators. Black Rats *Rattus rattus* were eradicated from Anacapa Island in 2001 and 2002 to restore seabird populations. For baseline and subsequent monitoring to assess the results of the rat eradication on Xantus's Murrelet populations, we developed population monitoring methods using a modified marine radar system and conducted nocturnal surveys to count the numbers of birds flying into or out of sample nesting habitats during the 2000 breeding season. High activity periods, activity zones and specific behaviors were examined for their ability to generate reliable data for a long-term population monitoring program. Radar is a useful tool to quantify the level of breeding activity in sample areas at nesting colonies and can be used to monitor population changes, to compare relative sizes of different colonies, to locate new breeding colonies, to confirm the continued existence of known historical colonies and to document use of specific nesting habitats at colonies.

Key words: California Channel Islands, introduced predators, radar, monitoring, rat eradication, *Synthliboramphus hypoleucus*, Xantus's Murrelets

INTRODUCTION

Xantus's Murrelets *Synthliboramphus hypoleucus* nest in loose colonies on the Channel Islands off southern California, USA, and islands off northwestern Baja California, Mexico (Hunt *et al.* 1980, Murray *et al.* 1983, Carter *et al.* 1992, Drost & Lewis 1995). The colonies are vulnerable to extirpation from breeding islands through predation by introduced mammalian predators (Jehl & Bond 1975, McChesney & Tershy 1998). Nest sites of Xantus's Murrelets occur mainly in rock crevices and to a much lesser extent under plants and artificial structures. At many colonies, a large proportion of nests occur in cliffs and steep slopes that are not easily accessible by humans without extensive climbing skill and equipment. Nest sites are visited only at night during the long incubation period (averaging 34 days), parents take long incubation shifts (one to six days), and eggs are periodically neglected (for one to four days). Chicks are precocial upon hatching and at two days old they depart from nest sites, accompanied by adults, for further rearing at sea (Murray *et al.* 1983). The birds' use of largely inaccessible island habitats and of nocturnal and non-daily nest visitations and their foraging far from shore makes it difficult to find colonies, estimate population size and monitor population changes.

In 1998/99, eradication of introduced Black Rats *Rattus rattus* at Anacapa Island in the northern Channel Islands, California, was planned by federal and state trustee agencies with funds obtained from the 1998 litigation settlement for the 1990 *American Trader* oil spill (ATTC 2001). Despite pioneering work to document the continued existence and approximate size of the Anacapa colony

during 1994–1997 (McChesney *et al.* 2000; H. Carter, unpubl. data), inadequate baseline data on the murrelet population existed to quantitatively measure changes in the population after rat eradication. During 2000–2003, a team of biologists developed new monitoring techniques and gathered baseline data for a long-term Xantus's Murrelet population monitoring program (ATTC 2001; Hamer *et al.* 2003; Whitworth *et al.* 2003, 2005).

Ornithological surveillance radar techniques were selected for application because they permit examination of bird activity in inaccessible habitats at Anacapa Island and have recently been applied to successfully monitor and study aspects of the biology of other seabirds in relatively inaccessible nesting habitats (Hamer *et al.* 1995, Burger 1997, Cooper & Blaha 1997, Cowen *et al.* 1997, Day & Cooper 1995, Burger *et al.* 2004). In past studies, radar units were mounted either on boats for offshore work or on a camper unit and four-wheel-drive truck for terrestrial work. Several types of radar have been effective tools in ornithological research for more than four decades (Eastwood 1967). Marine radar is probably the easiest and least expensive to operate and has additional benefits of high resolution, small minimal sampling range, high availability and high portability (Cooper *et al.* 1991, Hamer *et al.* 1995).

In this paper, we summarize radar monitoring techniques developed in 2000 to measure changes in the numbers of Xantus's Murrelets attending nest sites in inaccessible habitats in steep slopes and cliffs at Anacapa Island. We also report preliminary work at Santa Barbara and Santa Catalina Islands in 2000, which demonstrated additional uses for radar monitoring.

METHODS

Study area

Anacapa Island falls within Ventura County, California, and lies 15 km off the southern California mainland near Ventura (Fig. 1). Anacapa is the easternmost and smallest of the four northern Channel Islands. The island is composed of three small islets (West, Middle, and East Anacapa) managed by Channel Islands National Park (CINP). Waters extending 9.6 km offshore of Anacapa Island are managed by the Channel Islands National Marine Sanctuary (CINMS) and other agencies. The narrow island chain is approximately 7.5 km long with a 17.5 km perimeter of steep rocky slopes and cliffs, and is topped by flat or more gently sloping plains. The coastline harbors more than 100 sea caves (Bunnell 1993). West Anacapa Island is the largest in area (1.7 km²) and highest (284 m), followed by Middle Anacapa Island (0.6 km², 99 m) and East Anacapa Island (0.5 km², 73 m). In April and May 2000, we conducted radar surveys from the CINMS research vessel *Balleña* anchored off the south side of Middle Anacapa Island (34°00.322'N, 119°22.910'W), approximately 300 m off East Fish Camp, a semiprotected anchorage. The location provided approximately 1.5 km of radar coverage of potential coastal nesting habitats (16% of the total shoreline of Middle Anacapa Island and East Anacapa Island combined).

Santa Barbara Island lies 60 km southwest of Los Angeles but still within Santa Barbara County. The island is managed by CINP and the surrounding waters by CINMS and other agencies (Fig. 1). Santa Barbara Island is the smallest (2.5 km²; elevation: 193 m) of the four southern Channel Islands. The coastline of Santa Barbara Island consists of rugged sheer cliffs and steep rocky slopes topped by a gently sloping plain. We conducted a single radar survey at the island in April 2000 from the vessel *Balleña* anchored off the east side (33°28.983'N, 119°01.522'W), approximately 300 m off Landing Cove, a semiprotected anchorage. This location allowed approximately 1.6 km of radar coverage of potential coastal nesting habitats (12.0% of the total shoreline of Santa Barbara Island).

Santa Catalina Island, managed mainly by the Catalina Conservancy, lies about 30 km southwest of Los Angeles in Los Angeles County. In April 2000, we conducted a single survey aboard the vessel *Balleña* at the northwestern end of Santa Catalina Island, 400 m from Eagle Rock (33°27.892'N; 118°35.856'W) and north of Catalina Harbor. The sampled area has extensive steep slopes and cliffs and is highly exposed to prevailing northwest winds, without a protected anchorage (Fig. 1). This location provided approximately 1.6 km of radar coverage of potential coastal nesting habitats (4% of the total shoreline of Santa Catalina Island).

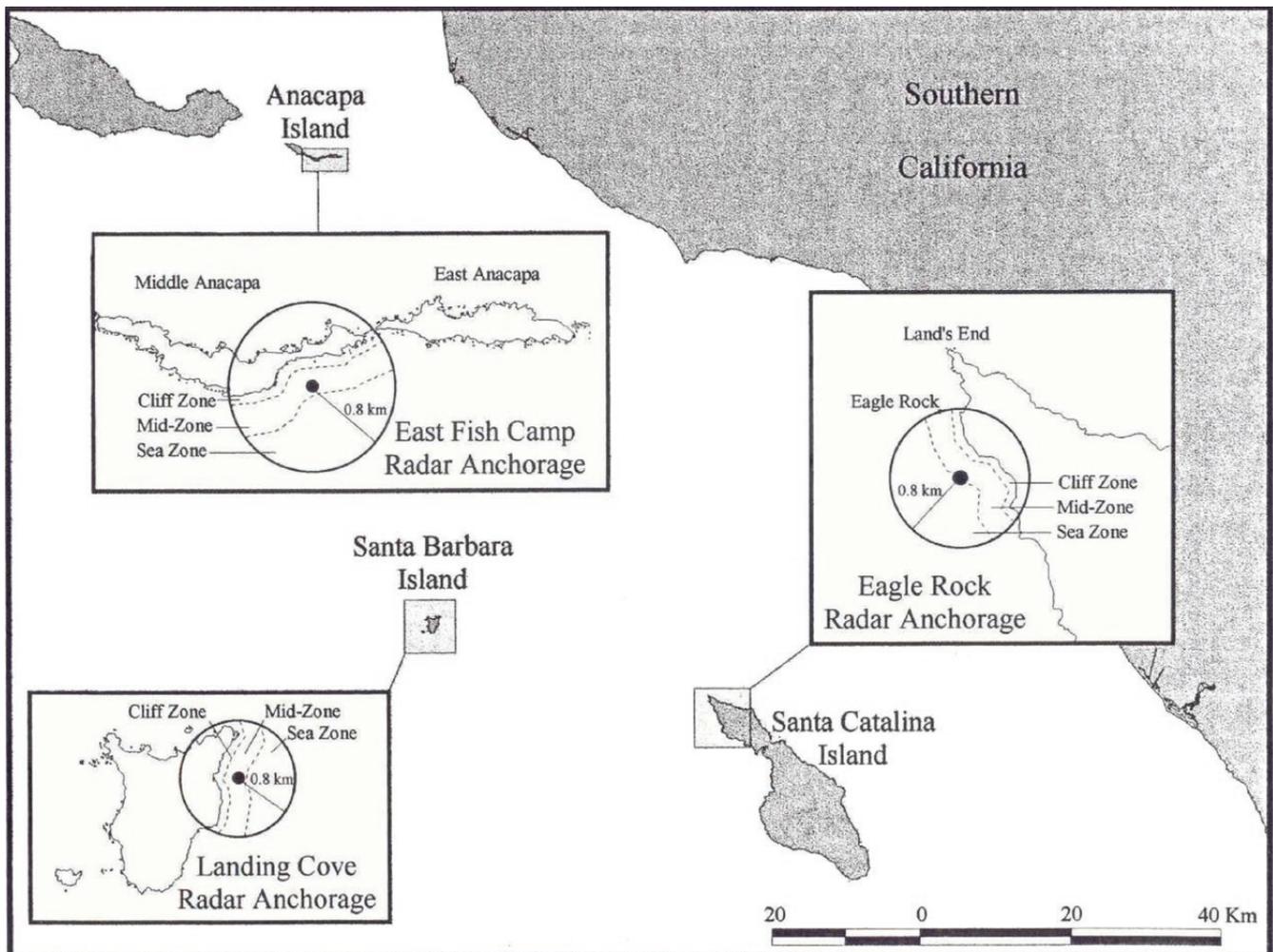


Fig. 1. Radar survey stations at Anacapa, Santa Barbara, and Santa Catalina islands in 2000, and activity zones sampled.

Radar equipment

Radar surveys were conducted using a model FCR-1411, 10-kW, X-band radar unit (Furuno Marine Electronics, Camas, WA, USA), with a flexible two-metre-long slotted waveguide array antenna. Pulse length could be set at 0.08, 0.6, or 1.0 μ s, depending on range setting. The radar beam had a vertical span of 25 degrees and a horizontal beam width of two degrees. The radar was mounted directly on the wheelhouse of the *Balleña*, about 4 m above sea level. All data in 2000 were collected under relatively calm sea conditions with a radar vertical tilt of 0–10 degrees. If increasing wave clutter prevented a complete four-hour survey from 23h00 to 03h00 (PDT), the survey was cancelled or the data were not used in analyses. We did not conduct surveys in weather conditions that caused radar clutter along 50% or more of the island coastline, which effectively obscured detections in the survey area. Because of the difficulty of detecting a relatively small murrelet-sized target at great distances with the radar, the 0.5 nm setting (1.1 km radius) was used as the most appropriate scale for monitoring. The radar completed one scan every 2.5 s with a plotting function set to 30 s. Therefore, each radar target would leave an echo trail with each echo retained for 30 s. The echo trail could be subsequently plotted and measured, allowing us to estimate flight speeds by using a handheld scale to measure the distance between three or more echoes.

Data collection

A biologist experienced in interpretation of radar echoes monitored the screen and recorded murrelet detections on a data sheet. Echoes on the radar screen were also recorded for the duration of each survey using a Sony (New York, NY, USA) 8-mm video camera so that biologists could review survey sessions at a later date.

In 2000, we monitored sites during the expected main incubation period in April and May, based on past average timing of breeding at Santa Barbara Island (Murray *et al.* 1983, Drost & Lewis 1995). Radar surveys were conducted throughout the night from 20h00 to 05h00 to document activity patterns. Weather conditions—including sea state, percent cloud cover, horizontal visibility (good, fair, poor), wind speed (km/h), wind direction, precipitation, air temperature (degrees Celsius), sea-surface temperature (degrees Celsius), cloud ceiling height (m) and moon phase (quarterly)—were recorded at the beginning and end of each survey period.

For each radar detection, we recorded identification number, time, activity zone, flight behavior, distance between echoes on the radar screen (mm), flight speed (km/h) and the number of radar echoes. All murrelet detections were segregated into three zones of activity (Fig. 1) when first observed:

- Cliff zone: within 100 m of the coastline
- Middle zone: within 101–400 m of the coastline
- Sea zone: more than 400 m from the coastline.

Large samples of flight paths in the cliff zone were plotted on US Geological Survey 7.5-minute topographic maps, when time allowed. Within the cliff zone, each detection was assigned one of four categories of flight behaviors:

- Inbound: flying towards the island within +45 degrees of a line perpendicular to the coastline
- Outbound: flying away from the island within +45 degrees of a line perpendicular to the coastline

- Circling: circling with a minimum 1/4 arc
- Unknown: flying parallel to coastline, at angles greater than 45 degrees of the coastline axis or without initial or final bearing from the shoreline

Species identification

Flight speed and echo size were used to identify Xantus's Murrelet radar detections. Targets with less than three echoes were not used because accurate flight speeds could not be calculated. When possible, four or more echoes were used to measure and calculate flight speed. To minimize the number of non-murrelet targets recorded, only birds flying 50 km/h or more were recorded as Xantus's Murrelets. The echo size of birds varied with the distance of the target from the radar and the orientation of the bird with respect to the radar. To help distinguish Xantus's Murrelets from other seabirds that frequently occurred in the nearshore region at Anacapa Island, daytime radar surveys in 2000 were conducted concurrently with an outside observer who gathered data on flight speed and echo size of other seabirds, including cormorants *Phalacrocorax* spp., Brown Pelicans *Pelecanus occidentalis* and Western Gulls *Larus occidentalis* (Hamer & Meekins 2002). Other seabird species somewhat similar in body size to the Xantus's Murrelet and known to fly at night included Ashy Storm-Petrels *Oceanodroma homochroa* and Cassin's Auklets *Ptychoramphus aleuticus*. To assist in confirming murrelet echoes, we identified a small sample of murrelet type echoes at night using both radar and simultaneous visual identification by personnel in inflatable boats.

Statistical analyses

We calculated hourly and nightly means, maximums, minimums, standard deviations and coefficients of variation (CVs) for radar detections. For hourly detection rates, we compiled total number of targets and total targets within four behavior categories. We then examined various behavior combinations by one-hour sampling period and presented estimates of the number of targets per hour for each sampling period. We graphically examined CV values for hourly detection rates for all nights combined to identify periods when CVs were lowest. To determine the percentage of the total variance in detection rate that occurred as variation between hours within nights (23h00–03h00) versus variation between nights, we used a nested variance component procedure. To determine if significant differences in mean hourly detections existed, we used ANOVA to test for differences between means. The above analyses were performed using the SPSS 10.0 for Windows statistical software (SPSS 1999) with $\alpha = 0.05$ for all tests. In addition, we tested for differences among islands in total nightly murrelet detections using a *t* statistic (t_s) designed for comparison of a single observation ($n =$ one night each at Santa Barbara Island and Santa Catalina Island) with the mean of a sample ($n =$ six nights at Anacapa Island; Sokal & Rohlf 1995: 227).

RESULTS

Sampling effort

Six nights of radar sampling from 20h00 to 05h00 were conducted at Anacapa Island between 10 April and 4 May 2000 (Table 1). Single nights of radar survey were conducted at Santa Barbara Island on 12 April and at Santa Catalina Island on 27 April (Table 1). A total of 80 hours of nocturnal radar sampling was conducted at colonies with an additional seven hours of diurnal sampling.

Species identification and flight speeds

Xantus's Murrelet average flight speed (all activity zones combined) was faster than other diurnal species examined, averaging 58.4 km/h [n = 1838; range: 45.0–98.2 km/h; standard deviation (SD): 8.4 km/h; Fig. 2]. The wide range of flight speeds probably reflects some birds flying at full speed and others at reduced speeds associated with take-off or landing on the water or at nest sites. All radar echoes (n = 12) recorded as Xantus's Murrelets and simultaneously observed on the water from an inflatable boat at night were confirmed as Xantus's Murrelets. For the 12 confirmed murrelets, the average flight speed was 54.6 km/h (range: 50.0–61.2 km/h). Flight paths of most murrelet targets in the cliff zone at Anacapa Island and Santa Barbara Island were heading directly into or away from (i.e. inbound or outbound) the shoreline of the island. Very few flight paths of birds flying parallel to the shoreline or circling were recorded (5.6% of all detections in 2000). Echo sizes of murrelet targets were relatively small at the 0.5 nm radar scale, varying from 2.0 mm to 2.5 mm in diameter.

Only cormorants (species unknown; three species occurred nearby during daylight hours) overlapped murrelet flight speeds, averaging 54.8 km/h (n = 75; range: 24.1–86.8 km/h; SD: 9.5 km/h; Fig. 2). However, cormorants most often flew parallel to the coastline during the day and were not observed from inflatable boats at night. Western Gull flight speeds averaged 35.6 km/h (n = 73; range: 12.9–49.9 km/h; SD: 5.1 km/h) and rarely attained 50.0 km/h, the lower end of Xantus's Murrelet flight speeds. Gulls also exhibited much larger radar echoes than Xantus's Murrelets. Brown Pelicans also had slower flight speeds than murrelets (average: 35.6 km/h;

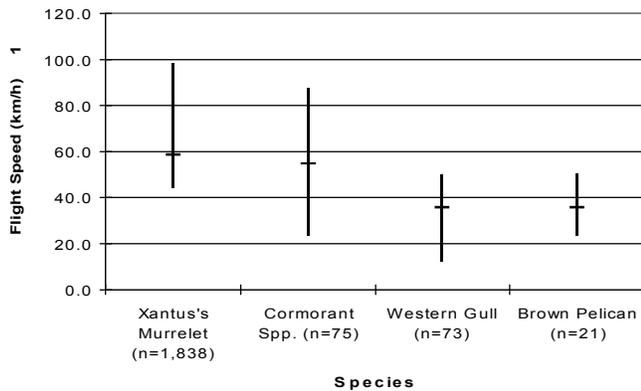


Fig. 2. Flight speeds (mean and range) for seabirds at Anacapa Island in 2000.

n = 21; range: 24.1–50.0 km/h; SD: 8.4 km/h; Fig. 2), a much larger radar echo and flight directions that paralleled the shoreline. Erratic and circling flight patterns of Ashy Storm-Petrels were sometimes observed by radar, but those birds had very small echoes on the radar screen (similar to bat echoes), and flight speeds were much slower than those of Xantus's Murrelets. Cassin's Auklets likely have flight speeds and radar echoes that are similar to Xantus's Murrelets, but no auklets were observed at night from inflatable boats and very few breed at Anacapa Island, away from the survey area (Whitworth *et al.* 2005).

Hourly and nightly variation in radar counts

Hourly detection rates within each survey night at Anacapa Island showed similar trends in activity levels (Fig. 3). Birds were not detected until after official sunset (mean sunset time: 19h35), but detections increased rapidly over the next few hours. Over eight days at three colonies, birds were first detected by radar at 20h32, 57 minutes after official sunset on 27 April. For six survey nights at Anacapa Island, the earliest detection occurred at 20h43 on 3 May, 64 minutes after sunset, and the latest detection was at 05h33 (1 May) 48 minutes before official sunrise at 06h21. The mean time of the earliest inbound and outbound detections in the cliff zone occurred at 21h05 and 21h06, respectively (n = six nights). The mean time of latest inbound and outbound detections in the cliff zone occurred at 05h05 and 05h02 respectively (n = five nights).

Except for 13 April, detection rates increased rapidly after 21h00, approximately 90 minutes after sunset, and usually peaked between 24h00 and 01h00. On 13 April, detection rates did not rise

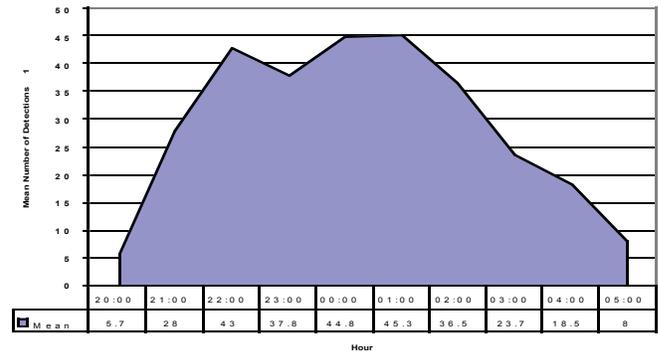


Fig. 3. Mean number of Xantus's Murrelet radar detections per hour (all behavior categories) at Anacapa Island for five nights of sampling in 2000.

TABLE 1
Xantus's Murrelet radar surveys at Anacapa, Santa Barbara and Santa Catalina Islands in 2000

Sampling site	Date	Detections (n)			
		Total, all zones	Cliff inbound	Cliff outbound	Total, cliff
East Fish Camp (Anacapa Island)	10 April	230	136	64	200
	13 April	289	83	117	200
	20 April	327	162	84	246
	1 May	324	88	106	194
	3 May	256	93	62	155
Eagle Rock (Santa Catalina Island)	4 May	305	138	60	198
	27 April	64	19	15	34
Landing Cove (Santa Barbara Island)	12 April	674	390	230	620

significantly until 23h00. Total radar counts were fairly consistent between 21h00 and 01h00. Hourly trends at Santa Barbara Island showed a pattern similar to that at Anacapa Island, with increasing detection rates after 21h00 and highest detection rates between 24h00 and 03h00 (Fig. 4). Most detections at Anacapa Island, Santa Barbara Island, and Santa Catalina Island occurred between 22h00 and 03h00. Detection rates for all nights dropped quickly after 03h00 and stayed relatively low until 05h30. At Anacapa Island, most birds had departed from nesting areas examined by radar and from at-sea congregations by 05h30. Unlike detection rates at Santa Barbara Island and Anacapa Island, the detection rate at Santa Catalina Island peaked between 22h00 and 23h00 ($n = 18$ detections/hour) and then dropped after 00h00.

Using a nested variance components analysis, variability among nights in detections at Anacapa Island accounted for 15.8% of the total variation; the remaining variation (84.2%) was attributable to variation among the sampling hours (23h00–03h00). Anacapa Island, Santa Catalina Island, and Santa Barbara Island exhibited significant differences in mean hourly detection rates (one-way ANOVA: $F = 63.57$, $df = 2$, $P < 0.000$), with overall means of 72.1, 16.0 and 168.5 detections per hour, respectively. The total detections (inbound and outbound combined; Table 1) on one night at Santa Catalina Island was significantly lower than the mean of nightly detections at Anacapa Island ($t_s = 5.28$, $df = 5$, $P < 0.01$). A similar test confirmed the higher rate of detections for Santa Barbara Island as compared with Anacapa Island ($t_s = 13.50$, $df = 5$, $P < 0.0001$).

The cliff zone exhibited consistent hourly detections through the night. The most consistent nightly counts and lowest CVs were obtained by combining inbound and outbound birds (hereafter “in/outbound”) for each hour or each night and by excluding circling

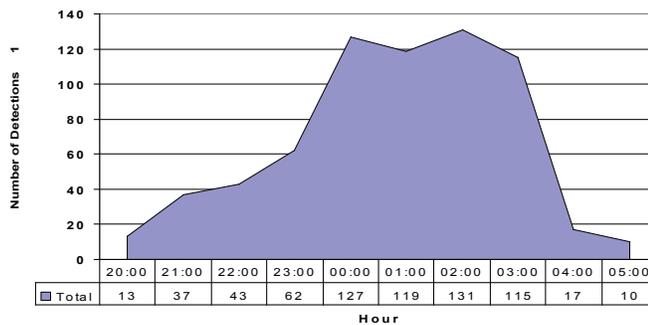


Fig. 4. Total number of Xantus's Murrelet radar detections per hour (all behavior categories) at Santa Barbara Island, 12–13 April 2000.

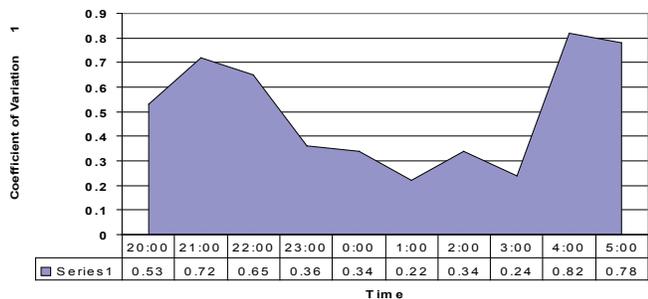


Fig. 5. Mean hourly coefficient of variation in Xantus's Murrelet detections at Anacapa Island for five nights of sampling in 2000.

or unknown behaviors. Similar consistency of counts between nights and low CVs were observed for total counts for all activity zones and behaviors. CVs were highest when nightly counts of in/outbound behaviors in the cliff zone were examined separately. CVs for in/outbound radar counts at Anacapa Island were lowest between 23h00 and 03h00 (Fig. 5). The mean hourly detection rate, minimum, maximum, SD and CV for in/outbound behaviors in the cliff zone at Anacapa Island were determined (Table 2). For 23h00–03h00, we observed no significant differences between mean hourly detection rates (one-way ANOVA: $df = 3$, $P = 0.661$).

DISCUSSION

Sampling effort and technique

Radar monitoring was found to be an effective method of gathering quantitative data on the numbers of Xantus's Murrelets flying into and out of sample nesting habitats at Anacapa Island, Santa Barbara Island and Santa Catalina Island. Standardized data for comparisons could best be obtained by limiting radar counts to the more protected near-shore zone where wave clutter is greatly reduced, sampling between 23h00 and 03h00, and using only in/outbound detections. The greatest limitation for conducting radar monitoring at Anacapa Island in 2000 was weather. Rough seas caused wave clutter (i.e. solid echoes from radar reflectance off the waves) on the screen, making it difficult to detect birds. Wind speeds of 24 km/h (13.0 knots) or more sometimes prevented complete surveys. In 2000, we reduced the effects of weather and corresponding wave clutter by selecting radar survey locations that had some protection from predominant northwest winds and by using data only from the more protected cliff zone for monitoring purposes. Subsequently (2001 and 2002), we modified radar deployment by improving vessel stern anchoring, by using a flux-gate compass and by modifying vertical radar tilt to 10 degrees or less (see below). Those improvements served to increase the number of nights of data collection annually (by allowing data collection during marginal conditions) and to improve data quality (by facilitating interpretation of echo trails). Successful survey nights occurred on 46%–67% of 24 potential survey nights in 2001 and 2002 (Hamer *et al.* 2003a).

TABLE 2
Xantus's Murrelet hourly detection rates (n) at Anacapa Island in 2000 for combined inbound and outbound behaviors in the cliff zone for five surveys combined

Time	Mean	Min	Max	SD	CV
20h00–20h59	5.0	3	8	2.65	0.53
21h00–21h59	18.6	3	34	13.46	0.72
22h00–22h59	33.8	8	61	21.90	0.65
23h00–23h59	26.2	17	39	9.44	0.36
00h00–00h59	31.2	17	47	10.78	0.34
01h00–01h59	30.4	21	38	6.58	0.22
02h00–02h59	23.6	13	34	7.96	0.34
03h00–03h59	13.8	8	16	3.27	0.24
04h00–04h59	13.6	1	23	11.10	0.82
05h00–05h59	7.5	1	13	6.24	0.78

SD = standard deviation; CV = coefficient of variation.

Despite various improvements, suitable protected anchorage sites will be the most important factor in the application of the radar monitoring approach to future monitoring at other locations at Anacapa Island and Santa Barbara Island, and at other islands. Long-term monitoring sites need to be somewhat protected from the weather to reduce the effects of wave clutter on the radar screen and shallow enough with suitable substrates to securely anchor. Shore-based radar monitoring could also serve as an alternative radar monitoring approach because it would eliminate problems with the availability of vessels and suitable anchorage sites. However, for some islands with steep rocky shorelines, few suitable sampling locations may exist.

After 2000, we made two modifications to compensate for the boat's movements at sea and to clarify on-screen images. We installed a Furuno model PG-1000 flux-gate compass and used a stern-anchoring system. On nights with high winds or strong currents, the vessel's position often shifted quickly, and sometimes it shifted because of anchor drag. Because of the rapidly changing radar image of the survey area, such movements made it more difficult to interpret and track individual echo trails. In 2001, we installed a PG-1000 flux-gate compass which fixed the image on the radar monitor regardless of the shifting position of the vessel. In 2002, CINP skippers also developed a functioning stern-anchoring system, which greatly reduced swing and anchor drag and helped to stabilize the boat.

In 2002, we also refined our radar-tilting protocol to minimize variation in murrelet detection rates during periods of poor weather. Modifications to our radar system allowed us to use a flexible waveguide to change the vertical angle of the radar antenna. By raising the antenna (in 5-degree increments) off the water, we could minimize wave clutter on the radar monitor. But because echo sizes of targets flying near the surface of the ocean became smaller and harder to detect as the antenna was raised, we established a maximum radar tilt of 10 degrees to minimize variation in radar detections. Through several 2002 trials under varying weather conditions, a tilt of 10 degrees or less was found to reduce wave clutter without reducing detection rates or increasing the difficulty of identifying murrelets. In 2002, to better standardize data collection, we determined that 50% or more of the shoreline must be free of wave clutter for the entire four-hour period to complete an adequate survey.

Species identification and flight speeds

Xantus's Murrelets likely represented almost all, if not all, birds with smaller echoes, high flight speeds and direct in/outbound flight lines detected by radar at night at Anacapa Island and Santa Barbara Island. Based on similar body size and flight speed, the one species most likely to be confused with the Xantus's Murrelets was the Cassin's Auklet; however, few if any auklets occurred in the radar-sampling areas. Nocturnal survey transects of at-sea congregations of Xantus's Murrelets from a small boat also did not detect any Cassin's Auklets or other species on the water that could be confused with Xantus's Murrelets (Whitworth *et al.* 2003).

Hourly and nightly variation in radar count

Counts of birds in the cliff zone best indicated breeding activity because these counts detected birds actually landing at (inbound) or departing from (outbound) nesting areas. Very few circling or unknown behaviors were recorded in the cliff zone because most flying murrelets appeared to be directly approaching or departing from land and were rarely seen sitting on the water in this zone.

Birds detected in the middle and sea zones were probably arriving at Anacapa Island or Santa Barbara Island from distant feeding areas, but they first attended at-sea congregations before flying up to nest sites in the cliff zone (Whitworth *et al.* 2003). Similarly, birds departing from nest sites may have attended at-sea congregations before departing from the island. Such behavior could cause double counting of individuals in middle and sea zones and recording of some birds that did not attend nesting areas. The cliff zone also exhibited consistent within-night patterns of hourly detections at Anacapa Island, Santa Barbara Island and Santa Catalina Island. Only in/outbound behaviors in the cliff zone were detected consistently through the night; circling and unknown behaviors were uncommon. These factors may explain why counts combining in/outbound behaviors within the cliff zone had the lowest nightly CVs.

We suggest use of the 23h00–03h00 sampling period for collection and analyses of radar count data for Xantus's Murrelets because highest mean counts were obtained in those hours, with lowest CV between nights. Mean counts with lowest CVs will likely have the greatest power to detect a population trend over time in any monitoring program (Hamer & Schuster 2003b). Therefore, such counts give the most reliable measure of nesting activity at Xantus's Murrelet nesting colonies, provide the best evidence of nesting activity at sites where evidence of nesting is lacking and provide the greatest power to detect population change over time (Hamer & Schuster 2003b). Results of the nested variance components analysis at Anacapa Island indicated that variability in detections between hours (23h00–03h00) far exceeded (*c.* 5:1) the variability in detections between nights. Therefore, radar studies with the objective of monitoring populations over time should attempt to sample all four hours of the peak activity period to control for hourly variation.

Nest monitoring at Anacapa Island in 2000 indicated a mean nest initiation date of 30 March (± 11 days; Whitworth *et al.* 2003), while radar surveys at Anacapa Island spanned 10 April to 4 May. Successful breeding adults can be expected to visit nest sites for a minimum of about 39–56 days, given a mean incubation period of 34 days (range: 27–44 days), plus a mean of eight days between laying of two eggs, a mean of two days between clutch completion and start of incubation, and a mean of two days from hatching to nest departure (Murray *et al.* 1983). In 2000, most nest site visitations at Anacapa Island would have been completed by 7–24 May. Therefore, radar surveys in 2000 were conducted during the peak incubation period with highest levels of nest visitations. Future monitoring by radar will have to take into account the differences in the annual timing of breeding of Xantus's Murrelets. Timing of breeding at Anacapa Island has been recently found to differ significantly from year to year, with murrelet nests initiated significantly later in 2004 and 2005 than in 2000–2003 (Whitworth *et al.* 2003, 2005).

The differences between Anacapa Island, Santa Barbara Island and Santa Catalina Island in hourly and nightly rates of murrelet detection by radar survey correspond to major differences in population size as estimated using nest searches and vocal detection surveys (Carter *et al.* 1992, 1997; Burkett *et al.* 2003; Whitworth *et al.* 2003). Using vocal detection surveys, at-sea congregations of murrelets had been previously discovered along the northwest coast of Santa Catalina Island in 1996 (H. Carter, unpubl. data), but no nests have been documented in that area. The description of in/outbound flight paths in 2000 by radar monitoring has provided additional information suggestive of breeding on the northwest side of the island.

Management implications

Our results show that radar is a useful tool for quantifying the relative level of breeding activity at nesting colonies. Using our approach, radar could be used to

- monitor population changes.
- compare relative sizes of various colonies by comparison of breeding activity.
- locate new breeding colonies.
- confirm the continued existence of known historical colonies.
- document portions of cliffs and bluffs being used for nesting at each colony.
- estimate densities of breeding birds for various portions of the coastline within a colony.

No differences in nightly mean count or CV were found among the four hours chosen as the sampling period. Therefore, for studies that do not involve long-term monitoring, we suggest that any of these hours could be used for exploratory work to locate and quantify additional sites at Anacapa Island, Santa Barbara Island or other islands. To survey several sites per night, the vessel could be moved to a new site after an hour of data collecting, and larger portions of an island could be covered in a short period with one radar-equipped vessel. A shorter sampling period would also help deal with rapidly changing weather conditions and perhaps eliminate the need to anchor the vessel, thereby increasing the number of successful survey nights with adequate weather conditions.

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HEALTH ASSESSMENTS AND STRESS RESPONSE OF XANTUS'S MURRELETS TO CAPTURE, HANDLING AND RADIO-MARKING

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SUMMARY

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Physiologic health of Xantus's Murrelets *Synthliboramphus hypoleucus*, a seabird of conservation concern in the United States and Mexico, has received little attention. During 1994–1997, we collected blood samples from murrelets attending nocturnal at-sea congregations adjacent to Santa Barbara Island, California, to establish baseline health indices. Hematologic and serum biochemistry indices were similar to those in other small alcids, except for lower creatine kinase activity, higher lactate dehydrogenase activity and higher uric acid concentration. To determine whether minimally invasive procedures for capture, handling and radio-marking pose a health risk to murrelets, we also assessed the acute stress response. Serum corticosterone, white blood cell counts (heterophils, lymphocytes, monocytes, eosinophils and basophils), and heterophil:lymphocyte ratio (H:L ratio) were used as biochemical and cellular indicators of stress. Corticosterone levels measured 30 minutes after capture (49 ± 22 ng/dL) were significantly higher than those measured within 3 minutes of capture (22 ± 21 ng/dL), indicating a stress response. However, at 30 minutes after capture, neither handling (before blood collection) nor sedation with isoflurane gas and radio-marking (subcutaneous anchor method) resulted in significantly higher mean corticosterone levels, indicating that the stress response was not greater in magnitude because of these additional procedures. White blood cell counts did not differ between any of the 30-minute study groups, but heterophil counts were higher, lymphocyte counts lower, and the H:L ratio higher for birds that were sedated and radio-marked. The magnitude of the stress response was not excessive relative to other handling protocols and probably did not cause changes to bird behavior after release.

Key words: Xantus's Murrelet, blood, health, stress, hematology, biochemistry, corticosterone, heterophil, telemetry, radio-marking, *Synthliboramphus hypoleucus*

INTRODUCTION

The Xantus's Murrelet (*Synthliboramphus hypoleucus*) is a small diving seabird (family Alcidae) that spends most of the year at sea and visits land only for a few months to breed (Murray *et al.* 1983, Drost & Lewis 1995). It has a relatively small global population and a geographically restricted breeding range in southern California, USA, and northwestern Baja California, Mexico. Populations appear to have declined considerably at several colonies since the late 19th century mainly because of predation and habitat degradation from introduced mammals, but marine threats (e.g. oil spills and light pollution) probably have seriously affected some colonies (McChesney & Tershy 1998, Carter *et al.* 2000, Burkett *et al.* 2003). World population estimates range from 10 000 to 20 000 breeding individuals (Drost & Lewis 1995, Carter *et al.* 2000, Burkett *et al.* 2003, Karnovsky *et al.* 2005, Keitt 2005), but potential threats from changes in local oceanographic conditions and prey availability, global climate change, and diseases have not been well described.

To better understand at-sea foraging and colony attendance, at-sea captures and two major radio-telemetry studies were conducted at Santa Barbara and Anacapa Islands, California (Whitworth *et al.* 1997, 2000a, 2003; Newman *et al.* 1999; Hamilton *et al.* 2005). During 1994–1997, we captured Xantus's Murrelets from at-sea congregations on the water beside Santa Barbara Island at night. Blood samples were collected

- to establish baseline health reference ranges (hematology and biochemistry) for Xantus's Murrelets, a species for which no such data exist and a species at risk of exposure to oil spills and possibly requiring biomedical care in the future.
- to determine the sex of individuals for telemetry studies.
- to obtain genetic material for assessment of genetic diversity.

We also gathered additional blood samples so that we could use blood corticosterone concentration, white blood cell estimates, and heterophil:lymphocyte ratios to evaluate acute stress response to various handling protocols. These techniques have been useful in

evaluating stress in other birds and mammals (Beuving & Vonder 1978; Harvey *et al.* 1980, 1984; Gross & Siegel 1983; Jain 1993; Maxwell 1993; Rijnberk & Mol 1997; Wingfield *et al.* 1997). In this paper, we report results from the health assessments and the acute stress response of Xantus's Murrelets to various handling protocols.

METHODS

Blood samples

We captured Xantus's Murrelets between 22h00 and 05h30 (PDT) off Santa Barbara Island, the largest breeding colony in the Southern California Bight (Drost & Lewis 1995), using the night-lighting technique (Whitworth *et al.* 1997). Birds (one or occasionally two at a time) were captured with a dip net and individually placed in cardboard holding boxes. Time of capture was recorded for every bird to the nearest minute. Before blood collection, all birds were evaluated for evidence of external trauma, physical impairments, emaciation or disease (e.g. oral or nasal discharge, respiratory compromise, infection, fecal discoloration) and for normal mucosal perfusion and handling response.

Blood samples (0.5–1 mL) were collected aseptically by a trained veterinarian (SHN) from the metatarsal vein using a 25-gauge needle and 3 cc syringe. After blood collection, a gauze sponge was used to apply pressure to the venipuncture site until hemostasis was complete. Immediately after blood collection, two blood smears were made using standard protocols (Jain 1986) and two Pre-Cal Microhematocrit tubes (Becton Dickinson, Rutherford, NJ, USA) were filled and clay capped for hematocrit and total solid determinations (Jain 1986). The remainder of the blood was placed in a Microtainer serum separator tube (Becton Dickinson) and centrifuged for 15 minutes at 3500 rpm using a Triac Centrifuge (Clay Adams, Sparks, MD, USA) to separate the serum from the cellular fraction. Disposable polyethylene pipettes were used to pipette serum into 1.5 mL cryovials (Out Patient Services, Petaluma, CA, USA). Samples were placed in liquid nitrogen until frozen and then stored in a –80°C freezer until analyzed.

Health assessments

Blood for hematology and serum biochemistry testing was collected during 6–11 May 1994, 26–29 April 1995, and 20–21 May 1995. Analyses were performed at Consolidated Veterinary Diagnostics Incorporated (CVD Inc., West Sacramento, CA, USA). White blood

cell (WBC) estimates and differential WBC counts (heterophils, lymphocytes, monocytes, eosinophils and basophils) were performed from Wright–Giemsa-stained blood smears. White blood cells were counted in an area on the smear where red blood cells (RBCs) were adjacent to one another (membranes touching but not overlapping). The average number of WBCs in ten high-power microscope fields (40×) was multiplied by 2000 to obtain the WBC estimate. Differential WBC counts were determined by counting 200 WBCs (at 40×) and multiplying the percentage of a particular cell type by the overall WBC estimate. Blood smears were also examined for RBC morphology, thrombocytes, reticulocytes and RBC parasites. Packed cell volume (PCV) and buffy coat were determined by microhematocrit centrifugation (Jain 1986). Total solids (TS) of plasma from centrifuged microhematocrit tubes were measured using a handheld temperature-regulated Schuco clinical refractometer (American Calduceus Industries, Carle Place, New York, NY, USA).

Serum was analyzed using routine biochemical methods to determine activities of alkaline phosphatase (Alk Phos), aspartate amino transferase (AST), creatine kinase (CK) and lactate dehydrogenase (LDH). Concentrations of albumin, globulin, total protein (TP), cholesterol, blood urea nitrogen (BUN), glucose, Ca, inorganic P, total CO₂, Cl, K, Na and uric acid (UA) were also determined. Albumin:globulin ratio (A:G ratio) was calculated. Protein electrophoresis was conducted to determine concentrations of the following globulins (alpha 1 and 2, beta 1 and 2, gamma 1 and 2), albumin and pre-albumin.

Stress study groups

Blood was collected from birds for part of the stress study during 26–29 April 1995, 20–21 May 1995, 15–19 April 1996 and 13–17 May 1996. Birds were transported to the larger support vessel within 10 minutes of capture and were randomly assigned into one of three experimental groups. In Group 1 birds (n = 32), blood samples were collected (see "Methods") within 10 minutes of capture. Group 2 birds (n = 54) remained in the holding box until 30 minutes after capture before blood sampling. Group 3 birds (n = 47) were removed from the holding box after capture and "handled" [i.e. morphometric measurements (culmen, tarsus, mass), brood patch inspection, photographs or facial plumage inspection, and banding] for up to 10 minutes before blood sampling at 30 minutes after capture.

TABLE 1
Xantus's Murrelet study groups, sample sizes and blood tests performed

Group	Blood collection time	n	WBC & differential cell count ^a	Serum biochemistry	Corticosterone assay
1	Sample at less than 10 minutes	32	Yes	Yes	Yes
2	Sample at 30 minutes	54	Yes	Yes	Yes
3	Handle & sample at 30 minutes	47	Yes	No	Yes
4	Radio-mark & sample at 30 minutes	56	Yes	No	Yes
5	Sample at less than 3 minutes	28	No	No	Yes
6 ^b	Sample at 60 minutes	28	No	No	Yes

^a As part of the stress evaluation, heterophil:lymphocyte ratios were calculated in samples when WBC and differential cell counts were performed.

^b Samples collected at 60 minutes are from the same birds sampled at less than 3 min. Because the sampling of individuals is repeated, statistical comparisons were not performed, and results are reported only for purposes of comparison.

WBC = white blood cell.

To obtain birds for two other study groups, other capture efforts took place during 10–12 April 1997 and 5–7 May 1997. Group 4 birds ($n = 56$) were radio-marked using subcutaneous anchor attachment under isoflurane sedation (Newman *et al.* 1999) before blood sampling

TABLE 2

Baseline health (hematology, biochemistry and electrophoresis) reference intervals for Xantus's Murrelets at Santa Barbara Island, California, 1994/95

Analyte	n	Mean±SD	Range
PCV (%)	49	51±3	48–55
TS	49	3.8±0.7	1.9–5.2
WBCs ($10^3/\mu\text{L}$)	60	6274±1918	4300–9500
Heterophils ($10^3/\mu\text{L}$)	60	3272±1835	1169–5180
Lymphocytes ($10^3/\mu\text{L}$)	60	2543±1329	1300–3990
Monocytes ($10^3/\mu\text{L}$)	60	228±216	12–480
Eosinophils ($10^3/\mu\text{L}$)	60	0±0	0–0
Basophils ($10^3/\mu\text{L}$)	60	160±236	13–424
Na (mEq/L)	12	154±3	148–160
K (mEq/L)	13	6.3±2.0	3.2–10.2
Cl (mEq/L)	13	116±6	102–122
Calcium (mg/dL)	17	8.0±0.7	6.8–9.6
P (mg/dL)	17	3.6±1.9	0.6–7.0
Total CO ₂ (mEq/L)	17	23±4	14–30
Alk Phos (IU/L)	26	48±48	5–165
AST (IU/L)	32	287±174	41–855
CK (IU/L)	31	46±45	15–348
LDH (IU/L)	31	396±232	112–839
Uric acid (mg/dL)	13	20.4±5.9	12.2–27.6
BUN (mg/dL)	26	3.6±0.9	1.2–5.8
Albumin (g/dL)	31	1.0±0.2	0.4–1.8
Total protein (g/dL)	32	3.2±0.4	2.2–4.7
Globulin (g/dL)	32	2.2±0.4	1.4–3.3
A:G ratio	32	0.5±0.2	0.3–0.9
Glucose (mg/dL)	32	374±85	158–564
Cholesterol (mg/dL)	31	288±50	160–351
Alpha 1 globulin (g/dL)	10	0.6±0.3	0.2–1.0
Alpha 2 globulin (g/dL)	10	0.1±0.2	0.0–0.5
Beta 1 globulin (g/dL)	8	0.4±0.15	0.2–0.6
Beta 2 globulin (g/dL)	9	0.0±0.1	0.0–0.2
Gamma 1 globulin (g/dL)	10	0.6±0.25	0.2–1.0
Gamma 2 globulin (g/dL)	10	0.0±0.0	0.0–0.0
Albumin (g/dL)	10	2.1±0.35	1.6–2.6
Pre-albumin (g/dL)	10	0.1±0.05	0.0–0.1
Mass (g)	35	168±11	150–186

PCV = packed cell volume; TS = total plasma solids; WBCs = white blood cells; Alk Phos = alkaline phosphatase; AST = aspartate amino transferase; CK = creatine kinase; LDH = lactate dehydrogenase; BUN = blood urea nitrogen; A:G = albumin:globulin.

30 minutes after capture. Group 5 birds ($n = 28$) were transported to the support vessel within two minutes of capture for immediate blood sampling within three minutes of capture, and were returned to a cardboard pet carrier. At 60 minutes after capture, birds were removed from the box and an additional blood sample was collected (Group 6). Because group 6 birds represented a repeated sampling of individuals, statistical comparisons of blood results were not performed, but results are reported for comparative purposes. To prevent possible predation, all murrelets were released approximately 500–1000 m away from the island at the completion of all procedures.

Stress parameters

Corticosterone concentrations were determined using the ImmuChem Corticosterone ¹²⁵I radioimmunoassay (Cat. 07–120102: ICN Biomedicals, Costa Mesa, CA, USA), which has been validated for accuracy and precision in avian samples (Spano *et al.* 1987, Vleck *et al.* 2000). All corticosterone assays were performed in duplicate; if paired results differed by more than 10%, the assay was repeated. Differential cell counts [heterophil (H), lymphocyte (L), monocyte, eosinophil and basophil] were performed, and the H:L ratio was calculated. Because 1995 and 1996 WBC estimates did not differ among study groups, this test was not performed on samples collected in 1997 (Table 1).

Statistical analyses

Descriptive statistics were performed using the BMDP Statistical Software (Los Angeles, CA, USA). Outliers were identified and removed using the range test (PetitClerc & Kelly 1981, Solberg 1994). Individual serum biochemical values were removed from the data set if the difference between the two highest (or lowest) values in the distribution exceeded one third of the range of all values. Hematologic intervals were established using the same method; however, individual differential WBC counts were not removed from the data set unless the overall WBC estimate for the individual bird was determined to be an outlier. Kruskal–Wallis analysis of variance and a modified Mann–Whitney rank sum test (Hollander & Wolfe 1973) were performed to determine whether statistical differences ($P < 0.05$) existed between groups 1–5.

TABLE 3
Mean corticosterone concentration (ng/dL) in Xantus's Murrelet study groups

Venipuncture time	Study group	n	Mean±SD	Range
Sample at less than 3 minutes	5	28	22±21 ^a	4–83
Sample at less than 10 minutes	1	32	33±12 ^{a,b}	13–57
Sample at 60 minutes ^d	6	28	46±29	1–114
Sample at 30 minutes	2	54	49±22 ^{b,c}	14–112
Handle & sample at 30 minutes	3	47	55±17 ^c	23–09
Radio-mark & sample at 30 minutes	4	56	79±61 ^c	20–269

^{a,b,c} Means marked with a common superscript are not statistically different (Kruskal–Wallis ANOVA and modified Mann–Whitney *U*-test, $P < 0.05$).

^d Samples collected at 60 minutes are from the same birds sampled at less than 3 minutes. Because sampling of individuals is repeated, statistical comparisons were not performed, and results are reported here only for purposes of comparison.

RESULTS

We calculated mean baseline health indices (hematology, biochemistry, electrophoresis and mass) from Xantus's Murrelets sampled in 1995 and 1996 (Table 2). Blood health indices indicate immune competence (WBC and cell counts, A:G ratio, globulin and gamma globulin concentrations), inflammation (WBC and cell counts, alpha and beta globulins), electrolyte and acid–base balance (Na, K, Ca, Cl, P, total CO₂), liver structure and function (AST, LDH, albumin and TP), kidney structure and function (AST, BUN, UA), muscle exertion or damage (Alk Phos, AST, LDH, CK), and nutritional status (cholesterol, glucose, TP).

Statistical differences ($P < 0.05$) the groups were identified for corticosterone concentration (Table 3). Lowest mean corticosterone concentration was measured from birds sampled within three minutes of capture (group 5), differing from all other study groups except for birds sampled 10 minutes after capture (group 1). Highest mean corticosterone concentration was found in birds that were sedated, radio-marked and sampled at 30 minutes (group 4), but significant differences were not found when those birds were compared to others sampled at 30 minutes regardless of handling procedures (groups 2 and 3).

Hematologic results that varied between the groups included relative frequencies of heterophils, lymphocytes, basophils and TS. Birds that were sedated, radio-marked, and sampled at 30 minutes (group 4) had significantly higher heterophil counts ($P < 0.05$;

Table 4) and lower lymphocyte counts (and therefore a higher calculated H:L ratio, 3.79) than did

- group 1 birds sampled less than 10 minutes after capture (H:L ratio: 1.11).
- group 2 birds sampled at 30 minutes (H:L ratio:1.34).
- group 3 birds handled and sampled 30 minutes after capture (H:L ratio: 1.91).

Group 4 birds also had a significantly higher basophil count than did other study groups. No differences were measured for monocyte counts, eosinophil counts or PCV.

DISCUSSION

Health assessments

One of the greatest threats to the health of marine birds is oil pollution, and increased efforts to rehabilitate oiled wildlife effectively have been a major reason for recent interest in establishing baseline blood health intervals. Because Xantus's Murrelets are highly vulnerable to oil pollution in the Southern California Bight and off central California (Carter *et al.* 2000, Carter 2003), they may require biomedical care in the future because of petroleum exposure or other environmental contaminants. They also may fall ill because of diseases or algal blooms. Baseline blood reference intervals will serve as the health standard for determining how ill birds are while in care and when they will be healthy enough for release (Newman & Zinkl 1998, Mazet *et al.* 2002, Newman *et al.* 2003).

TABLE 4
Hematology (mean \pm standard deviation) of Xantus's Murrelets at Santa Barbara Island, California, 1994/95

Analyte	Group 1	Group 2	Group 3	Group 4
	Sample at less than 10 min	Sample at 30 min	Handle & sample at 30 min	Radio-mark & sample at 30 min
WBCs ($10^3/\mu\text{L}$)	6824 \pm 1996 ^a (n=34)	6134 \pm 1835 ^a (n=53)	7028 \pm 2396 ^a (n=45)	6377 \pm 2490 ^a (n=57)
Heterophils (cells/ μL)	3383 \pm 1897 ^a (n=34)	3312 \pm 1522 ^a (n=53)	4237 \pm 1787 ^{a,b} (n=45)	4604 \pm 2122 ^b (n=56)
Lymphocytes (cells/ μL)	3047 \pm 1350 ^a (n=34)	2467 \pm 1193 ^{a,b} (n=53)	2217 \pm 1342 ^b (n=45)	1214 \pm 1077 ^c (n=56)
Monocytes (cells/ μL)	330 \pm 236 ^a (n=34)	212 \pm 184 ^a (n=53)	275 \pm 254 ^a (n=45)	314 \pm 318 ^a (n=56)
Eosinophils (cells/ μL)	2 \pm 10 ^a (n=34)	0 ^a (n=53)	0 ^a (n=45)	3 \pm 20 ^a (n=56)
Basophils (cells/ μL)	62 \pm 158 ^a (n=34)	136 \pm 218 ^a (n=53)	295 \pm 342 ^a (n=45)	328 \pm 113 ^a (n=56)
PCV (%)	51 \pm 4 ^a (n=28)	50 \pm 4 ^a (n=32)	49 \pm 4 ^a (n=24)	50 \pm 6 ^a (n=52)
Field TS (g/dL)	3.8 \pm 0.7 ^a (n=28)	4.0 \pm 0.7 ^{a,b} (n=32)	4.1 \pm 0.9 ^{a,b} (n=24)	4.4 \pm 1.1 ^b (n=52)

^{a,b,c} Means marked with a common superscript in the same row are not statistically different (Kruskal–Wallis ANOVA and modified Mann–Whitney U -test, $P \leq 0.05$)

WBCs = white blood cells; PCV = packed cell volume; TS = total plasma solids.

Diseases such as avian botulism, West Nile virus, and exotic Newcastle disease have been documented in shorebirds and marine birds in southern California (Reece 1989, Docherty & Friend 1999, Hansen 1999, Rocke & Friend 1999) and also pose a real threat to the health of Xantus's Murrelets. The recent emergence of the highly pathogenic H5N1 avian influenza has further increased concern about the effects that diseases may have on free-ranging bird populations such as Xantus's Murrelets. From this perspective, baseline health intervals also will serve as a valuable tool to determine whether rehabilitation is an option or whether euthanasia is more humane. As better knowledge of the small population size of Xantus's Murrelets at specific colonies is gained, it may be extremely important to treat individuals if they represent a unique genetic component of the species. In this case, baseline health intervals will be invaluable.

Baseline health indices have been established for many avian species, but information on diving marine birds, particularly alcids, is lacking because of the difficulty of capturing and sampling these species. Fortunately, some comparative data are available for other small alcids, including Marbled Murrelets *Brachyramphus marmoratus* and Cassin's Auklets *Ptychoramphus aleuticus* (Newman *et al.* 1997, Newman & Zinkl 1998). Xantus's Murrelets have generally similar reference-range blood results to those of Marbled Murrelets and Cassin's Auklets with the following exceptions:

- Xantus's Murrelets had lower CK activity than both Marbled Murrelets and Cassin's Auklets.
- Xantus's Murrelets had higher LDH activity level than Marbled Murrelets.

CK and LDH both become elevated with muscle contraction and exertion or with physical struggling, and higher LDH activity in Xantus's Murrelets may indicate that this enzyme is a more sensitive indicator of physical exertion for this species. Based on LDH alone, our results suggest that Xantus's Murrelets undergo a greater level of struggling during capture by night-lighting than either Marbled Murrelets captured by night-lighting or Cassin's Auklets captured by hand or mist net.

Xantus's Murrelet hematology and serum biochemistry reference intervals were established from birds sampled in 1994 and 1995, the latter being a poor year for food availability, which led to colony abandonment (Whitworth *et al.* 2000a, Roth *et al.* 2005, Schwemm *et al.* 2005). Although food resources were not adequate near Santa Barbara Island for successful reproduction by many birds in 1995, Xantus's Murrelets preserved their own health by maintaining physiologic homeostasis, apparently by foraging very far from the colony and greatly reducing colony attendance by abandoning incubation duties. If birds were undergoing emaciation and muscle catabolism associated with starvation and ecologic conditions, one would expect both CK and LDH to be elevated, and other blood chemistry changes to be apparent, but this was not the case. Although sample sizes were small in both 1994 and 1995, no noticeable differences in blood results were observed between years, and the birds were considered healthy in both years. In 1996 and 1997, when additional samples were collected for the stress study, breeding success and prey availability were much improved (Whitworth *et al.* 2000a, Roth *et al.* 2005, Schwemm *et al.* 2005).

Stress response

Stress is defined as the physiologic response to stimuli perceived as a threat (real or anticipated). The stress response is manifested

through physical, behavioral and physiologic changes, including increased heart and respiratory rates and nearly simultaneous release of corticosterone and epinephrine (Harvey *et al.* 1984). Acute stress results in corticosterone release mediated through activation of the hypothalamic-pituitary-adrenal axis (Harvey *et al.* 1984). Avian blood samples collected less than three minutes after capture (group 5) represent background corticosterone levels for unstressed conditions (Beuving & Vonder 1978, Schoech *et al.* 1998, Wingfield & Romero 2000, Romero & Romero 2002). Corticosterone concentration in blood is believed to rise continuously until it reaches a plateau, at which time the animal either escapes from the stressful situation, adapts to the stressor, suffers adrenal exhaustion or undergoes pathologic changes that can result in death (Harvey *et al.* 1984, Smith *et al.* 1994, Rijnberk & Mol 1997). The rise in corticosterone associated with handling is routinely used to assess the magnitude of the stress response, with more stressful situations causing a greater rise in corticosterone (Silverin 1998). Concurrent with adrenal response in birds is a cellular response in which heterophil counts increase and lymphocyte numbers decrease (Maxwell 1993).

Mean corticosterone concentration from Xantus's Murrelets in this study revealed that the stress response was initiated within 10 minutes of capture, but mean corticosterone concentration was not significantly higher than background level (under three minutes) until 30 minutes after capture (Table 3). At 60 minutes, mean corticosterone concentration was slightly lower than at 30 minutes. This observation suggests that the capture-associated stress response peaked between 10 and 30 minutes, and reached a plateau between 30 and 60 minutes when birds behaviorally and physiologically adapted to being captured. Without ongoing or additional stressful stimuli, Xantus's Murrelets showed no additional increase in corticosterone levels, suggesting that murrelets could continue to be held under appropriate conditions [i.e. in the dark in pet carriers, with little exposure to auditory or visual stimuli, and at moderate temperatures (10°C–15°C) without a subsequent increase in stress response]. However, to ensure that murrelets were not affected, we did not examine the stress response beyond 30 minutes for birds that underwent handling and procedures.

Corticosterone levels measured from all study groups bled at 30 minutes after capture (Table 3) suggested that neither handling birds before blood collection, nor sedating them with isoflurane gas and radio-marking them with subcutaneous anchors resulted in significantly higher mean corticosterone concentrations than those seen in birds kept in holding boxes until sampling at 30 minutes. However, a cellular response was detected as heterophils increased and lymphocytes decreased in association with sedation and subcutaneous anchor radio-marking. This observation demonstrated that the H:L ratio was a sensitive marker of cellular change associated with handling procedures in Xantus's Murrelets.

The subcutaneous anchor attachment method (Newman *et al.* 1999) is commonly used to evaluate habitat use and movements of small alcids (Whitworth *et al.* 1999, 2000a, 2000b; McFarlane Tranquilla *et al.* 2003; Ackerman *et al.* 2004; Adams *et al.* 2004; Peery *et al.* 2004) and to conduct post-release survival studies on oiled and rehabilitated seabirds (Anderson *et al.* 2000, Golightly *et al.* 2002). In most cases, this technique has not been considered to have had significant short- or long-term behavioral or physiologic effects on birds, but this conclusion has been difficult to prove. In our study, although radio-marked Xantus's Murrelets (group 4) had the highest mean corticosterone concentration, the level was not statistically

different from that of all other birds sampled at 30 minutes after capture. This finding suggests that the stress associated with sedation and subcutaneous anchor attachment was not greater than the stress associated with being captured, handled and blood-sampled at 30 minutes. In other radio-marked bird species, the stress response also has been found to be limited. For instance, fecal glucocorticoid levels of Dickcissels (*Spiza americana*) were elevated for only 24 hours after harness radio-marking (Suedkamp Wells *et al.* 2003).

Sedation using isoflurane inhalant anesthetic probably reduced the pain and stress associated with radio attachment using subcutaneous anchors and may even reduce the stress associated with capture and handling. Heatley *et al.* (2000) found that corticosterone concentrations in manually restrained Amazon Parrots *Amazona ventralis* were significantly higher than for birds anesthetized using isoflurane. Once sedated, the "perceived threat" that regulates corticosterone levels is impeded and, if stress occurs, sedation can be important in preventing resulting effects.

Some debate continues about the degree of behavioral effects associated with the subcutaneous anchor radio attachment technique (McFarlane Tranquilla *et al.* 2003, Ackerman *et al.* 2004, Hamel *et al.* 2004, Peery *et al.* 2004). For Xantus's Murrelets, the magnitude of the immediate stress response associated with this procedure was not found to be extreme. In fact, transitory corticosterone levels observed in Xantus's Murrelets undergoing radio-marking were comparable to those in Black-legged Kittiwakes *Rissa tridactyla* during chick rearing (Kitaysky *et al.* 1999). Although differences in stress response between species can be expected, it is highly unlikely that the stress response associated with a once-per-life event (e.g. subcutaneous anchor radio-marking) could result in a life-threatening outcome. These levels of stress can be experienced by birds annually for months during periods of low prey availability, although such conditions typically develop gradually.

Because handled Xantus's Murrelets had only a slightly higher mean corticosterone level than non-handled birds and because the stress response did not continue to rise between 30 and 60 minutes after capture, birds apparently did not experience an overwhelmingly detrimental stress response associated with these techniques. Based on the stress-mediated corticosterone response, our handling protocols did not pose any immediate danger to the health of Xantus's Murrelets and can be safely used in future studies. However, possible behavioral effects may occur from various other sources (e.g. physical effects of radio attachment on flying or diving, temporary changes in waterproofing, and brief disruption of social activity).

CONCLUDING REMARK

Although baseline health indices have been established for Xantus's Murrelets at Santa Barbara Island, California, we recommend that additional baseline health assessments be conducted at other major colonies in southern California, USA, and northwestern Baja California, Mexico. Health and stress issues can vary between colonies, and establishing baseline information for each colony will allow detection of subtle differences and changes in health before catastrophic mortality conditions occur—especially oil spills. With the potential emergence of avian influenza in North America, disease screening should also become a standard part of

future health assessments. Such research will promote a greater understanding of how diseases and other stressors affect the health of Xantus's Murrelets throughout their breeding range.

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CHARACTERISTICS OF DIVING IN RADIO-MARKED XANTUS'S MURRELETS

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SUMMARY

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We monitored diving activity of radio-marked Xantus's Murrelets *Synthliboramphus hypoleucus* near Anacapa Island, California, during the breeding season. Thirteen radio-marked murrelets were remotely monitored from Anacapa Island with a handheld antenna and radio receiver for 29 hours in three sample periods in April and May 2003. Mean dive durations in the sample periods were $18 \text{ s} \pm 2 \text{ s}$, $28 \text{ s} \pm 2 \text{ s}$, and $24 \text{ s} \pm 4 \text{ s}$, suggesting that dives were less than 21 m from the surface. Dive duration and subsequent time on the surface differed between the sample periods. Dive duration and subsequent time on the surface were not correlated in observations stratified by individual bird or by sample period. Further, dive duration and subsequent time on the surface were not correlated within foraging bouts. Dive characteristics measured near Anacapa Island suggested that Xantus's Murrelets have the ability to capture prey found at varying depths, but will feed on prey that is most available near the surface of the water.

Key words: Xantus's Murrelet, *Synthliboramphus hypoleucus*, Anacapa Island, radio telemetry, dive duration, dive depth, surface times

INTRODUCTION

Xantus's Murrelets *Synthliboramphus hypoleucus* are found near islands off the west coast of Baja California and within the Southern California Bight during the breeding season from March through June (Jehl & Bond 1975, Hunt *et al.* 1979, Briggs *et al.* 1987, Drost & Lewis 1995). Like other alcids, they are wing-propelled pursuit-divers and forage almost exclusively by diving (Ashmole 1971, Gaston & Jones 1998). They feed in small, dispersed groups, usually in singles and pairs, but occasionally in groups of up to eight individuals (Howell 1910, Hunt *et al.* 1979, Drost & Lewis 1995). They feed on small fish and zooplankton and may use prey concentrated near the surface in ocean fronts and along convergence lines (Hunt *et al.* 1979, Hamilton *et al.* 2004, Hamilton 2005). At-sea distribution of murrelets relative to nesting colonies is variable within and between years (Whitworth *et al.* 2000, Hamilton 2005). Presumably this variation occurs because abundance, distribution, depth and availability of prey are patchy and variable in the Southern California Bight (Mais 1974, Roesler & Chelton 1987, Cross & Allen 1993). Rather than feeding at fixed depths, murrelets may exercise flexibility in the depth and length of time they spend underwater to obtain prey. Prey depth, availability and flexibility in foraging behaviors can be inferred from an examination of dive duration, time on the surface following a dive, variation in dive duration between time periods and within foraging bouts (series of consecutive dives), and variation in dive duration among individuals (Wanless *et al.* 1997, Jodice & Collopy 1999). These diving characteristics have not yet been examined for Xantus's Murrelets. In 2003, we examined the diving characteristics of radio-marked Xantus's Murrelets near Anacapa Island, California, during the breeding season.

METHODS

Anacapa Island (34°01'N, 119°24'W) is the easternmost of the northern four Channel Islands in the Southern California Bight. In 2001/02, Black Rats *Rattus rattus* were eradicated from Anacapa Island to protect Xantus's Murrelet (hereafter murrelet) nests from depredation (American Trader Trustee Council 2001). An estimated 200–600 murrelet pairs nest on Anacapa Island (Whitworth *et al.* 2003). During 14–16 April and 28–29 April 2003, we captured 44 murrelets from within nocturnal congregations near Anacapa Island using a night-lighting capture technique (Whitworth *et al.* 1997). Radio transmitters (model PD-2, Holohil Systems, Woodlawn, Ontario, Canada) were attached to murrelets using a subcutaneous anchor technique (Mausser & Jarvis 1991, Newman *et al.* 1999). In conjunction with this project, we also examined at-sea distribution, nocturnal colony attendance and foraging habitat of the 44 radio-marked murrelets (Hamilton 2005).

We used a three-element Yagi antenna and receiver (model R-4000: Advanced Telemetry Systems, Isanti, MN, USA) to remotely monitor diving activity from Anacapa Island during three sample periods of one to three days each. To select a radio-marked bird to monitor, we scanned all 44 frequencies with the receiver to determine which transmitters could be detected with a strong signal. We then randomly selected and monitored one of the detected frequencies for at least 30 minutes. During each monitoring session, we estimated sea state using the Beaufort scale. Transmitter signals were detected when the bird was on the surface and were interrupted when the bird dove (Wanless *et al.* 1993). Thus, we considered a dive to start when the radio signal became inaudible and to end when the signal was once again audible.

Start time and end time of each dive were voice recorded on a tape recorder. A dive was defined as a signal loss of more than four seconds, because in Marbled Murrelets *Brachyramphus marmoratus*, shorter signal losses were reported only when waves over-topped the birds, when preening activities resulted in the antenna dipping underwater or when birds executed very short dives (Jodice & Collopy 1999). Jodice & Collopy (1999) found that shorter signal losses represented only 3.3% of all signal losses, and so we believe that few potential dives were discarded by using the four-second criterion. A surface interval was defined as less than three minutes between successive dives, and a foraging bout was defined as three or more consecutive dives that ended with an interval of more than three minutes (Jodice & Collopy 1999). Diving efficiency was calculated as the ratio of dive duration to subsequent surface interval (Wanless *et al.* 1988). When we could record a complete foraging bout, the number of dives per bout was calculated. Percentage of time underwater during a foraging bout was estimated as the quotient of dive duration over foraging bout duration. We determined these diving characteristics for the monitored murrelets: dive duration, surface interval, diving efficiency, duration of foraging bout, number of dives per foraging bout and percentage of time spent underwater during each foraging bout.

We used two-way analysis of variance (ANOVA: SPSS, version 11.5, 2002, Chicago, IL, USA) to test for differences in dive duration between the sample periods. Because repeated dives were recorded for each bird, we controlled for pseudoreplication by using the bird as a factor in the two-way ANOVA. We used two-way ANOVA to also test for differences in surface intervals between the sample periods. We used single-factor ANOVA, where the mean for the individual bird was the experimental unit, to compare mean diving efficiency, duration of foraging bout, number of dives per foraging bout and percentage of time spent underwater during each foraging bout between sample periods.

We used analysis of covariance (ANCOVA) to determine whether there was a relationship between dive duration and subsequent surface interval for individual birds and by sample period (SAS Institute, 2001, Cary, NC, USA). A strong relationship between dive duration and subsequent surface interval was expected if the bird was diving to maximum effort or depth as limited by physiology (Jodice & Collopy 1999). To determine whether there was a relationship between dive duration and subsequent surface interval for individual birds within foraging bouts, we averaged dive durations and surface intervals by foraging bout, and tested for differences between foraging bouts and between birds. We treated dives by the three birds recorded in two sample periods as separate samples because we found significant differences between sample periods in dive duration and surface intervals.

We estimated the direction of each bird from Anacapa Island by estimating the direction of the strongest signal. To estimate the location of the radio-marked murrelets during diving trials, we determined the maximum distance that a radio transmitter on the surface of the water could be detected from the island. On 28 April 2003, two transmitters were attached to 470 mL plastic bottles half-filled with water. The bottles were floated on the surface at various locations and were recorded using a global positioning system [GPS (model 12XL, Garmin, Olathe, KS, USA)]. Each time the transmitters were placed on the surface, an observer with a receiver and handheld antenna on Anacapa Island determined whether they could be detected. Distance from each test location to the observer

was calculated using a Geographic Information System (GIS) program (ArcView 3.3, ESRI, Redlands, CA, USA).

RESULTS

During 19–20 April, 9–11 May, and 24–26 May 2003 (periods 1, 2, and 3 respectively), diving activity of radio-marked murrelets was monitored for a total of 29 hours. Diving occurred across all daylight hours (06h00–20h00 PDT; Table 1). Sea state was mild during all monitoring sessions [Beaufort 1 (1–3 knots) or 2 (4–6 knots)], with the exception of 9 May (within Period 2), which scored a Beaufort 6 (22–27 knots). In total, we recorded 447 individual dives and 23 complete foraging bouts for 13 murrelets during the three sample periods. All of the murrelets were south of Anacapa Island where water depth ranged from 50 m to 700 m. Based on our assessment of transmitter range, we estimated that the murrelets were detected only when they were within 5 km of the island.

Dive duration varied between the three periods ($F = 75.0$, $P < 0.001$, $df = 2$) and between individuals ($F = 2.8$, $P = 0.001$, $df = 12$), but we observed a significant interaction between period and individual ($F = 5.9$, $P = 0.016$, $df = 1$). The shortest dives were in period 1: 18 ± 2 s [mean \pm standard error (SE)]; the longest dives were in period 2: 28 ± 2 s. Dive duration in period 3 was 24 ± 4 s. Surface interval varied between periods ($F = 7.3$, $P = 0.001$, $df = 2$) and between individuals ($F = 3.7$, $P < 0.001$, $df = 12$), and we observed no interaction between period and individual ($F = 1.5$, $P = 0.220$, $df = 1$). The surface intervals in period 1 were shorter (14 ± 5 s) than those in period 2 (22 ± 8 s) and period 3 (24 ± 12 s).

There were no significant differences between the three periods in diving efficiency, duration of foraging bouts, number of dives per foraging bout and percentage of time spent underwater (Table 2). There was no relationship between dive duration and surface interval for individuals (ANCOVA: $F = 1.34$, $n = 16$, $P = 0.18$), or for the three periods (ANCOVA: $F = 0.91$, $n = 3$, $P = 0.41$), and there was no relationship between average dive duration and surface interval within a foraging bout for individuals (ANCOVA: $F = 0.10$, $n = 5$, $P = 0.98$).

TABLE 1
Number of dives per minute and monitoring effort for radio-marked Xantus's Murrelets from Anacapa Island, California, during three sample periods in 2003

Time of day (PDT)	Number of dives per minute (total minutes monitored)		
	19, 20 April	9, 10, 11 May	24, 25, 26 May
06h00–08h00	—	0.37 (90)	0.10 (175)
08h00–10h00	0.65 (120)	0.23 (220)	0.42 (55)
10h00–12h00	—	0 (50)	0.17 (180)
12h00–14h00	1.67 (15)	0.20 (40)	0.23 (110)
14h00–16h00	—	0.27 (15)	0.24 (225)
16h00–18h00	—	0.35 (190)	0.18 (60)
18h00–20h00	—	—	0.12 (200)
Time spent monitoring (hours)	2.25	9.75	17
Murrelets monitored (n)	4	8	4

DISCUSSION

Based on the allometric relationship between maximum diving depth and body mass developed by Schreer & Kovacs (1997) for alcids, the predicted maximum diving depth of murrelets would be approximately 25 m. This value is similar to the estimated diving depths for the murrelets in the present study. Based on average dive duration, and assuming that the average swimming speed was 1.5 m/s or less as measured for Thick-billed Murres *Uria lomvia* (Lovvorn *et al.* 1999), murrelets likely dove to depths of less than 21 m to capture prey. Smaller divers are not expected to swim as fast as larger ones, and thus swimming speeds of murrelets are not expected to be greater than those of the larger Thick-billed Murres (Lovvorn & Jones 1991, Schreer & Kovacs 1997).

Because water depth where the murrelets were foraging was greater than 50 m, birds must have been foraging within the water column and not on the bottom. Murrelets likely exhibited V-shaped dives, representing capture of single prey items; U-shaped dives, with a horizontal phase at shallow depths; or underwater undulations (rapid depth changes) during dives, indicating pursuit of prey and possibly ingestion of multiple prey items within a single shallower dive (or some combination of these). Thick-billed Murres foraging on epibenthic and epipelagic prey were shown to use U-shaped dives with a clear horizontal phase (Watanuki *et al.* 2001). Rhinoceros Auklets *Cerorhinca monocerata*, which feed on prey types similar to those observed for murrelets (euphausiids and epipelagic schooling fishes; Hamilton *et al.* 2004), were shown to exhibit both underwater undulations and V-shaped dives to capture prey within the water column (Kuroki *et al.* 2003). Although Rhinoceros Auklets exhibited longer dives (mean \pm standard deviation: 53 \pm 8 s) than the murrelets in this study, the median diving depth of the auklets was only 14.0 \pm 1.8 m. Thus, seabirds that feed on epipelagic prey may spend time pursuing prey in the water column rather than spending time diving to maximum depths. Duration and depth of dives in pursuit-diving seabirds are generally less than the maximum attainable (Burger 1991).

Dive duration and surface intervals for murrelets were similar to those for Ancient Murrelets *S. antiquus* observed foraging within two kilometres of a nesting colony in water less than 100 m deep (Gaston 1992), and Marbled Murrelets foraging within one

kilometre from shore where water depths ranged from three metres to 50 m (Carter & Sealy 1990, Strachan *et al.* 1995, Jodice & Collopy 1999, Henkel *et al.* 2004). Despite differences in foraging habitats, these three similar-sized murrelet species would be expected to exhibit similar diving durations because dive duration and maximum depth of dives are correlated with body mass (Piatt & Nettleship 1985). Further, all three species feed on small schooling fishes and euphausiids and are considered to be generalist feeders (Sealy 1975, Gaston 1992, Gaston *et al.* 1993, Gaston & Jones 1998, Hamilton *et al.* 2004). They probably feed on the prey types that are most available near the surface of the water.

Diving efficiency was slightly less than the value of 2.3 reported for Marbled Murrelets in central California (Henkel *et al.* 2004), 2.0–3.0 for Marbled Murrelets in Oregon (Jodice & Collopy 1999), and 3.9 for Marbled Murrelets in British Columbia (Carter & Sealy 1990). Diving efficiency should decrease with increasing dive duration and depth of dives (Wanless *et al.* 1988, Wanless *et al.* 1997, Jodice & Collopy 1999), and such a decrease could occur as a result of reduced prey availability near the surface of the water. Thus, prey may have been less available to the murrelets in this study.

Assuming aerobic diving, subsequent surface intervals are expected to increase as dive duration increases so that the bird can recover and replenish oxygen stores (Lea *et al.* 1996). The lack of correlation between dive duration and subsequent surface interval within foraging bouts for individual birds and between the three periods indicates that the murrelets did not dive to their maximum depth as limited by physiology or maximize the amount of time they could have spent underwater to obtain prey (Lea *et al.* 1996). This suggests that prey were available and able to be located and captured at less than maximum effort during the time of this study. Stronger relationships between dive duration and surface intervals may occur in years when prey availability is reduced and capture effort must be increased. This has been shown to occur in Adélie Penguins *Pygoscelis adeliae*, Common Murres *U. aalge* and European Shags *Phalacrocorax aristotelis* (Chappell *et al.* 1993, Wanless *et al.* 1993, Monaghan *et al.* 1994).

The shortest average dive durations and surface intervals occurred in period 1, suggesting that prey may have been more available earlier in the breeding season. The ability of murrelets to capture

TABLE 2

Summary of diving characteristics measured for radio-marked Xantus's Murrelets from Anacapa Island, California, during three sample periods in 2003 (mean \pm standard error)^a

	19, 20 April	9, 10, 11 May	24, 25, 26 May	F Value	P Value
Diving efficiency	1.8 \pm 0.2 (n=4) ^b	1.8 \pm 0.2 (n=8) ^b	1.8 \pm 0.3 (n=4) ^b	0.02	0.98
Duration of foraging bout (min)	4.7 (n=1) ^c	8.7 \pm 1.5 (n=6) ^c	7.5 \pm 0.8 (n=4)	0.79	0.49
Number of dives per foraging bout	10 (n=1)	13 \pm 3 (n=6)	9 \pm 2 (n=4)	0.60	0.57
Percent of foraging bout spent underwater	61 (n=1)	59 \pm 4 (n=6)	57 \pm 8 (n=4)	0.08	0.93

^a Each bird represents a sample unit within a period.

^b The total number of individual birds monitored was 13. Three birds were monitored in two separate sample periods.

^c Sample size includes only birds for which complete foraging bouts were recorded.

prey may be reduced when turbidity of the water increases as a result of windy conditions (Jodice & Collopy 1999). Thus, the longest average dive durations in period 2 may have been a result of the windy conditions that occurred on 9 May.

The lack of correlation between dive duration and surface intervals also suggests that murrelets used flexible foraging techniques and captured prey found at varying depths. Strong relationships between dive duration and surface intervals have been shown to occur in seabirds that feed on the bottom such as Red-legged Cormorants *P. gaimardi* (Frere *et al.* 2002). Variability in dive durations and surface intervals has been shown to occur in Neotropical Cormorants *P. brasilianus* that exhibit more flexible foraging techniques in that they forage both on the bottom and on pelagic schooling fishes (Quintana *et al.* 2004). Our data do not suggest that murrelets were feeding at the bottom; however, they do indicate that the murrelets foraged at varying depths and pursued prey underwater for varied amounts of time. Several studies have shown that diving depth of seabirds is positively correlated with dive duration (e.g. Wanless *et al.* 1997, Luna-Jorquera & Culik 1999, Mills 2000, Kuroki *et al.* 2003). However, this correlation did not occur in Marbled Murrelets and may not occur in murrelets or other seabirds that forage throughout the water column (Jodice & Collopy 1999).

There were several indications that prey resources were abundant and available near Anacapa Island in 2003. Nesting murrelets exhibited high hatching success (88%), and densities of murrelets attending nocturnal congregations adjacent to the island were high in comparison with other years (Whitworth *et al.* 2005). Among all 44 radio-marked murrelets from Anacapa Island (13 sampled for this study), 88% of at-sea locations were within 40 km south of the island (Hamilton 2005). In other years, murrelets have been documented foraging farther from nesting colonies (Whitworth *et al.* 2000, Hamilton 2005). Some of the 44 radio-marked murrelets in 2003 were associated with ocean fronts that were 10–30 km south of Anacapa Island and persisted for at least three weeks until mid-May (Hamilton 2005). Ocean fronts concentrate zooplankton and schooling fish near the surface of the water (Owen 1981, Olson & Backus 1985, Mann & Lazier 1996). Although the murrelets that we monitored were feeding less than 5 km south of Anacapa Island, they may have been responding to the same upwelling, because seabird associations may extend up to 9.3 km beyond fronts (Hofer 2000). It was unknown whether the murrelets foraging farther than 5 km from the island exhibited similar dive characteristics or if they needed to dive deeper to obtain prey. Our results suggest that murrelets have the ability to capture prey at varying depths. However, when prey are available near the surface of the water, the murrelets will probably feed on that prey.

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