Black-vented Shearwater

Puffinus opisthomelas

FRENCH: Puffin cul-noir SPANISH: Pardela mexicana

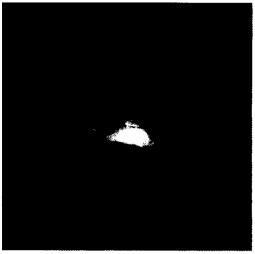
his small shearwater, endemic to the Pacific Coast of North America, is named for the dark under tail-coverts that separate it from other closely related "white-vented shearwaters" in the genus *Puffinus*. Like most other *Puffinus* species, the Black-vented Shearwater is nocturnal when visiting land. When sandy substrate is not available for burrowing, this species lays its single white egg at the back of a natural rock crevice. Appearing deserted during the day, nesting colonies come alive with the moaning wail of shearwaters during moonless nights.

In contrast to its more pelagic relatives, the Black-vented Shearwater is a coastal species, most frequently observed within 25 km of shore. It is the only shearwater that breeds at sites within the California Current, nesting on remote desert islands near productive up-

The Birds of North America

Life Histories for the 21st Century welling zones off the west coast of Baja California, Mexico. In feeding, this shearwater plunges from just above the sea surface or submerges from afloat and dives to depths >20 m to catch schooling fishes, squid, and probably crustaceans.

A paucity of information on the breeding biology and status of this bird led the International Union for the Conservation of Nature (IUCN) to list it as a Species of Concern and Mexico to list it as Threatened. Although recent information shows that populations are larger than previous estimates



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suggested, >95% of the breeding population occurs solely on Natividad I., Baja California Sur, Mexico. In addition, all breeding locales have historically had introduced mammals and permanent human residents, a situation that has reduced available nesting habitat and increased adult mortality.

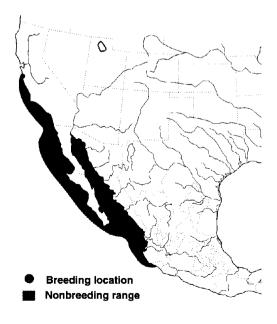


Figure 1.
Distribution of the Black-vented Shearwater.

The coastal foraging habits of this species and its erratic postbreeding dispersal stand in contrast with many other Puffinus shearwaters, making this an interesting species for study. Very little is known about the bird, owing primarily to its breeding on remote islands, and its nocturnal, burrow-nesting habits. Besides a collection of egg records from the 3 breeding islands, knowledge of reproduction is limited almost entirely to Natividad I. (Keitt 1998). However, postbreeding movements northward are well known from observations off California, and these movements have been linked to ocean temperatures (Ainley 1976, Briggs et al. 1987, Tyler et al. 1993, Ainley et al. 1995, Veit et al. 1996). Future research on foraging energetics and food provisioning of young of this coastal species should prove rewarding.

DISTINGUISHING CHARACTERISTICS

Small shearwater (length 35–38 cm, wingspan 76–89 cm, mass about 400 g), characterized by darkbrown upperparts, blending with mostly dull-white underparts; mostly white underwings, with smudgy-brown trailing edges; and brownish under tail-coverts. Amount and extent of mottling along sides of neck, shoulders, and flanks are highly variable. Plumage of both sexes identical. Dark bill is slender, long, and sharply hooked. Tarsus is laterally compressed; legs and feet are dusky flesh-colored. Males tend to be larger than females, though not significantly so (see Measurements, below; see Table 2). Females can be sexed after laying by distended cloaca (Serventy 1956).

Member of the Manx Shearwater (Puffinus puffinus) complex, comprised of 8 closely related forms having together a global distribution and widely debated taxonomy. Generally similar in plumage to Pink-footed Shearwater (P. creatopus), but Blackvented is smaller with faster wingbeat and lacks arcing flight pattern of Pink-footed. Most easily confused with Manx (P. puffinus), Townsend's (P. auricularis auricularis), and Audubon's (P. lherminieri) shearwaters. Manx and Townsend's are black-backed with strongly demarcated white underparts, in contrast to brown-back and smudgy sides of Blackvented. Manx has white under tail coverts that extend up sides and are visible when bird is on the water. Audubon's and Townsend's have dark under tail coverts like Black-vented. Audubon's and Townsend's are smaller-bodied than Black-vented. Townsend's has white flank patches. Flight styles of these species vary with wind speed and direction and bird behavior making this a poor characteristic for field identification (S. Howell pers. comm.).

Observed plumage aberrations include whitevented forms, pale or dusky vented forms (D. Shearwater pers. comm.), several leucistic individuals from s. California, and one pure albino individual photographed in Monterey Bay, CA, by Jim Lomax (D. Shearwater pers. comm.).

DISTRIBUTION

THE AMERICAS

Breeding range. Figure 1. Breeds on islands off Pacific Coast of Baja California, Mexico, including Natividad I. (27.5°N, 115.25°W), San Benito Is. (28.25°N, 115.5°W), and some rocks offshore of Guadalupe I. (29.0°N, 118.5°W; Everett 1988). Historical breeding sites include Λsunción (Am. Ornithol. Union 1957) and San Martín Is. (Am. Ornithol. Union 1998), but these reports are not well documented and probably erroneous (Everett 1988), and recent surveys show that this species does not presently breed on either Asunción or San Martín (Keitt 1999).

Nonbreeding range. Common along entire Pacific Coast of Baja California north to central (Alta) California (Point Conception, 34°50′N). Usually occurs within 25 km of coast (Everett 1988); viewed as frequently from land as from boats (Stallcup 1976). In years of increased ocean temperature in e. Pacific, large numbers disperse to Monterey Bay, smaller numbers farther north (Everett 1988). Five specimens were collected in late 1800s at Vancouver I., British Columbia (Kermode 1904); there are unsupported reports of individuals at mouth of Columbia River (Anthony 1896).

Occurs regularly in central Gulf of California, with slight peak in Sep and Oct (Tershy et al. 1993).

Range south of Cape San Lucas is confounded by difficulties in distinguishing this species from the similar Townsend's and Audubon's shearwaters. Willett collected specimens off the coast of Jalisco, Mexico (Everett 1988), and Pitman (1986) reported sightings off the coast of Nayarit, Jalisco, and Colima, Mexico. Jehl (1974) collected a specimen in Apr 1973 off the coast of Guerrero, Mexico (specimen no. 38461, San Diego Natural History Museum).

OUTSIDE THE AMERICAS Not recorded.

HISTORICAL CHANGES

Historical breeding range not well known. Reported to breed on Guadalupe I., Mexico (Anthony 1900), but possibly extirpated there by feral cats (*Felis catus*; Everett and Pitman 1993), which were reported depredating Black-vented Shearwaters on that island in 1892 (Anthony 1896). At present, the only known active colonies are on offshore islets of Guadalupe I.: Afuera and Negro (Everett and Pitman 1993). Unconfirmed breeding reports for San Martín (Howell 1910, 1911, Am. Ornithol. Union 1983) and San Geronimo (Nelson 1921) Is. on west coast of Baja California

and Georges (Leigh 1941) and Raza (Bancroft 1927) Is. in Gulf of California. All of these reports appear erroneous (Everett 1988).

FOSSIL HISTORY

Oldest fossil representative of this group is *Puffinus raemondonckii* (Van Beneden 1871) from deposits of early Oligocene. Most modern *Puffinus* species groups evolved by middle Miocene (Olson 1985). Brownbacked shearwaters—Fluttering (*P. gavia*), Balearic (*P. puffinus mauretanicus*), Black-vented, and Yelkouan (*P. puffinus yelkouan*)—are thought to have speciated from an ancestral stock that was isolated as the Tethys Sea broke up in the Tertiary period (Bourne et al. 1988).

SYSTEMATICS

The term "puffin" appears to be derived from the Middle English word "pophyn" from the Middle Ages, which referred to the fat, cured carcasses of nestling shearwaters prepared for food. Because of the proximity of nesting shearwaters and Atlantic Puffins (*Fraterculaarctica*), confusion eventually arose and the name "puffin" was applied as the common name of that species. Puffin has remained associated with the shearwaters, and there are now about 15 species in the genus *Puffinus*.

Type specimen of this species was collected by John Xantus, 20 Jul 1859, off Cape San Lucas, Baja California Sur, Mexico (Coues 1864). This is a member of the Puffinus puffinus complex that traditionally has confused taxonomists (Brooke 1990). Most early citations refer this species to P. opisthomelas (Coues 1882, Loomis 1918, Am. Ornithol. Union 1931). Murphy (1952) and Jouanin and Mougin (1979) reorganized the complex and placed Black-vented Shearwater as subspecies, P. p. opisthomelas, of Manx Shearwater (Am. Ornithol. Union 1957). However, Am. Ornithol. Union (1983: 24) treated the Black-vented as a separate species, stating, "It seems best to consider (the entire complex) as allospecies of a superspecies." Most taxonomists presently maintain species status for the Black-vented Shearwater (Am. Ornithol. Union 1998).

GEOGRAPHIC VARIATION; SUBSPECIES

None reported. Historically considered a subspecies of Manx Shearwater (Murphy 1952, Am. Ornithol. Union 1957). At present, considered distinct species with no subspecies recognized.

RELATED SPECIES

Black-vented was placed in subgroup *Puffinus* with Fluttering, Hutton's (*P. huttoni*), Yelkouan, and Balearic shearwaters by Kuroda (1954) on the basis of behavior, osteology, external morphology, distribution, and fossil record. Molecular phylogenetics of the *Puffinus* subgroup reveal that *P. gavia* and *P.*

huttoni have consistent phylogenetic association, as do *P. p. yelkouan* and *P. p. mauretanicus* (Austin 1996). The Black-vented was not included in this work, and its affiliation remains obscured.

The 8 species that historically made up the P. puffinus complex can be separated into 2 groups by current distribution, external morphology, breeding season, and migration pattern (Bourne et al. 1988, Brooke 1990). Black-backed forms include Manx, Townsend's, Newell's (P. auricularis newelli), and Hutton's. These species are similar in that they often nest in the mountains, lay in late spring, feed offshore, and have extensive migration. Brown-backed forms include Balearic, Yelkouan, Fluttering, and Blackvented. These species nest mostly on coastal islets, lay in early spring, are primarily inshore feeders, and are relatively sedentary (Brooke 1990). Of these species, all are found in Northern Hemisphere except Hutton's and Fluttering. Back color is considered a retained character in several discussions on the evolution of this group (Murphy 1952, Bourne et al. 1988). Blackbacked forms are suggested to have dispersed and speciated in westward pattern from ancestors in n. Atlantic; brown-backed forms dispersed in easterly direction and speciated in the following order: Balearic, Yelkouan, Fluttering, Hutton's, Black-vented (Murphy 1952).

MIGRATION

NATURE OF MIGRATION IN THE SPECIES

Many individuals remain near breeding areas yearround (Am. Ornithol. Union 1957). Known to attend colony at least 10 mo of year (Keitt 1998). Some disperse north and south after completion of breeding in Jul or Aug, remaining close to shore.

TIMING AND ROUTES OF MIGRATION

No classic migratory behavior is known for this species. It is known to attend Natividad colony in some numbers at least Nov through Aug. In late Dec 1996, burrows showed >90% occupancy (Keitt 1998). Most dispersal occurs after breeding is complete, in Jul or Aug, much of it northward. Species most common off s. California in Nov, Dec, and Jan, with peak abundance in Dec. Individuals found north of Point Conception, CA, Jul through Dec, with peak abundance in Oct and Nov (Ainley 1976). Reports for Oregon coast mid-Sep–Nov (Gilligan et al. 1994). Nine records for this species off Vancouver I., BC, between 1891 and 1986, most in Jul–Nov. A Feb record in 1895 appears anomalous for its season (Campbell et al. 1990).

In Gulf of California, observed Jan through Jun, with slight peak in abundance Sep-Oct (Tershy et al. 1993).

MIGRATORY BEHAVIOR

No regular migration known; typically stays within 25 km of shore (Am. Ornithol. Union 1983, Everett and Pitman 1993). Most often seen in flight; may rest on water when wind is very light.

A sighting off Cordell Banks, 40 km offshore near San Francisco, CA, was exceptional for its distance from shore (Stallcup 1990). Individuals regularly reach Point Conception, off central California (1,000 km north of breeding islands), but extent of northward movements appears related to water temperature (Ainley 1976). Greatest abundance off California from San Diego to Monterey in years with above-average temperatures (Ainley 1976, Briggs et al. 1987, Tyler et al. 1993, Ainley et al. 1995, Veit et al. 1996).

Reported to prefer waters >14°C (Ainley 1976). Northern distribution and abundance appear to be influenced by warm-water events. Between 1955 and 1973, reported in California coastal waters (San Diego to Bodega Bay) every year except 1955 and 1956; over 10-fold variation in abundance in these years. Maximum relative abundance in 1967, 1970, and 1971, all years with above-normal temperatures (Ainley 1976).

Between 1987 and 1995, this species showed 2 peaks in abundance off s. California (between San Diego and San Luis Obispo Co.): fall 1990 and winter 1993. These peaks were significantly correlated with increased ocean temperatures and showed a 3-mo time lag from peak temperatures (Veit et al. 1996). Surveys off s. California in Apr and Jun, 1987–1994, showed peak density (0.3 bird/km²) of this species in Apr 1992 (Ainley et al. 1995). Off central California (San Luis Obispo Co. to Bodega Bay), surveys in Jun of same time period showed peak densities of 0.001 bird/km² in 1986, 1993, and 1994 (Ainley et al. 1995). Mean density of this species off s. California (Point Conception to San Diego) in Dec reported as 0.09 bird/km² ± 0.30 SE (Tyler et al. 1993). Density of birds in fall 1977 off Oceanside in s. California reported to be as high as 80 birds/km², yielding peak population estimates in the area of 20,000-30,000 individuals (Briggs et al. 1987).

In Monterey Bay, CA, species not reported in fall 1996, when sea surface temperatures were <13.5°C. In 1997, first observed there in Oct, with abundance peaking in Nov, when sea surface temperatures were 16.5–17°C (S. Benson unpubl.). In fall 1998, a warm water year, reported to be common north to Marin and Sonoma Cos., where usually rare to absent (S. Howell pers. comm.).

HABITAT

BREEDING RANGE

Breeds on remote desert islands that have little vegetation and no native mammalian predators

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(Fig. 2). Nesting habitat is primarily open, with small shrubs and cacti in areas suitable for burrowing. On Natividad I., habitat consists of stabilized dunes covered with introduced ice plant (Mesembryanthemum crystallinum); on San Benito and Guadalupe Is., primarily rocky outcrops. Nests in burrows on Natividad I.; on San Benito Is. and offshore rocks of Guadalupe I., uses rock crevices more commonly (Everett 1988, BSK). All current nesting islands are <200 m in elevation; majority of nest sites are at elevations <50 m (BSK). Natividad, San Benito, and offshore rocks of Guadalupe Is. are located in areas of strong, year-round upwelling (Huver 1983, Tyler et al. 1993). On the basis of fishery catches, even during years of low abundance of sardines (Sardinops spp., an important forage fish; see Food habits: diet, below) along west coast of North America, sardines are abundant near the colonies and in central Gulf of California (Lluch-Belda et al. 1989). Semipermanent cyclonic eddies occur north and south of Point Eugenia, the prominent point on Baja California coast 3 km south of Natividad I. (Hewitt 1981). These eddies may help concentrate prey for Black-vented Shear-

Effects of annual variation in physical environment near breeding colonies not known.

WINTER AND MARINE RANGE

Coastal waters from Monterey, CA, to central Mexico. Generally prefers waters >14°C (Ainley 1976). Occupies waters primarily over continental shelf. Depths near breeding colonies increase greatly away from shore, and likely some individuals forage in waters over 2 km in depth. Wide continental shelf north of colonies and inside of Channel Is. in s. California indicate that this species spends majority of time in waters <200 m in depth. This area between Point Eugenia, Baja California, Mexico, and Point Conception, Alta California, coincides with the greatest numbers of Black-vented Shearwaters and has distinct warm-temperature marine fauna; species composition changes north and south of these headlands (Hubbs 1960).

Use of local or small-scale hydrographic features is undescribed in the species.

FOOD HABITS

FEEDING

Main foods taken. Small, schooling bait fish (mostly anchovies and sardines [Clupeiformes]) and squid (Keitt et al. 2000).

Microhabitat for foraging. Surface down to 50 m depth (Keitt et al. 2000). Swallows whole prey below surface; likely swallows 1 prey item / dive, as reported for Townsend's and Newell's shearwaters (Ainley et al. 1997).

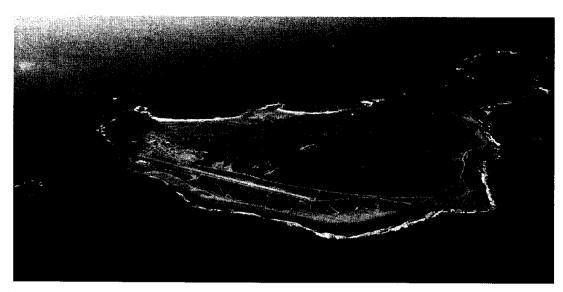


Figure 2. Aerial view of Natividad Island (looking northwest) — the main Black-vented Shearwater nesting colony. Note airstrip in foreground, town at left; the colony encompasses all of the lighter areas (e.g., not in darker areas showing mountain ranges). Photo by the Cooperative Buzos y Pescadores.

Food capture and consumption. Feeds by pursuitplunging (shallow dives from air), dipping, seizing prey on surface from floating position, and diving (submerging and using wings to propel underwater). Puffinus shearwaters have strong pincerlike bills, and their tongues and palates are lined with retrose papillae (back-facing bumps), which are well adapted for catching and holding prey (Warham 1990). A compressed tarsus and narrow pelvis promote efficient diving (Kuroda 1954).

Observed to follow boats using chum to attract birds, though Black-venteds do so less than Sooty (*P. griseus*), Short-tailed, and Pink-footed Shearwaters (D. Shearwater pers. comm.). Not reported to feed on bait refuse (Everett 1988) and does not take anchovies thrown overboard as chum, even though other species of shearwaters do (D. Shearwater pers. comm.).

Observed feeding by plunging into foamy crests of waves off west coast Baja California (Anthony 1896), though this behavior reported to be unusual (Everett 1988). In Monterey Bay, CA, regularly observed to feed by plunging in the foamy wake created by herds of Common Dolphins (*Delphinus delphis* and *D. capensis*). In these events the Black-vented is described as the predominant shearwater in a mixed flock including Sooty, Pink-footed, and some Flesh-footed (*P. carneipes*) Shearwaters (D. Shearwater pers. comm.).

Shearwaters may use olfaction to help locate prey (Warham 1990). Black-vented Shearwaters were shown to have a large olfactory bulb in the brain, similar in relative size to that of Black-footed Albatross (*Diomedea nigripes*) and considerably greater than those of landbirds (Wenzel and Sieck 1972). Black-vented Shearwaters showed changes in respiratory rate when

exposed to olfactory stimuli, suggesting advanced sense of smell (Wenzel and Sieck 1972).

DIET

Main contents of regurgitations from adult birds (presumed breeders) on Natividad I. were northern anchovies (Engraulis mordax) and Pacific sardines (Sardinops sagax; Keit et al. 2000). A few regurgitations also contained squid (order Teuthoidea) beaks. Identification of regurgitated fish is difficult because they are swallowed headfirst and are partially digested when regurgitated, leaving prey without heads and otoliths. Items regurgitated, collected during chick provisioning, are probably for provisioning young. No information on whether adult diet differs from chick diet.

Gizzards collected from birds depredated by cats on Natividad I. contained otoliths of northern anchovies and squid beaks from family Mastigoteuthidae (Keitt et al. 2000).

Stomachs of birds collected in Monterey Bay, CA, in Dec 1910 contained sardines (Everett 1988). Reported feeding on sardines near Los Coronados Is. (25 km southwest of San Diego; Stephens 1921). Large flock (12,000 birds) observed feeding on spawning squid off La Jolla, CA, in Nov 1979 (Unitt 1984).

FOOD SELECTION AND STORAGE

Puffinus shearwaters are known to render food into stomach oil, which often is fed to chicks (Lockley 1942, Warham 1990). This is thought to be an adaptation to increase efficiency of offshore foraging by concentrating energetic value of food (Warham 1990). Black-vented Shearwater is unlikely to regurgitate oil for chicks because it forages so close to shore.

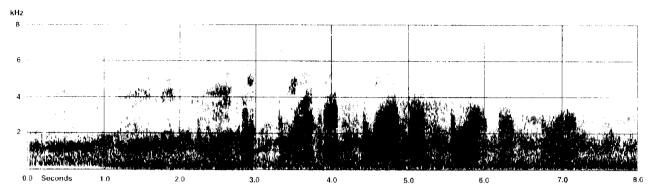


Figure 3. Vocalizations of the Black-vented Shearwater. Recorded by B. Tershy on Natividad I., Baja California Sur, Mexico, 19 Apr 1997. Prepared by staff of Borror Laboratory of Bloacoustics, Ohio State University, using a Kay Elemetrics DSP Sona-Graph 5500 (with 150-Hz effective frequency resolution and 200-point FFT transform size).

NUTRITION AND ENERGETICS

Not studied in this species, but probably similar to nutrition and energetics of Wedge-tailed (*Puffinus* pacificus) and Manx shearwaters (see Lee and Haney 1996, Whittow 1997).

METABOLISM AND TEMPERATURE REGULATION No information.

DRINKING, PELLET-CASTING, AND DEFECATION

No information. In similar Manx Shearwater, adults are known to drink seawater (Witherby et al. 1943), and juveniles are reported to drink seawater vigorously after fledging (Lockley 1942).

SOUNDS

VOCALIZATIONS

Because this species is not sexually dimorphic and all social activity on the colony occurs at night, vocalizations are probably an important part of individual recognition, courtship, and pair-bond maintenance. This phenomenon has been well studied in Manx Shearwater, which is known to have sexually dimorphic vocalizations (Brooke 1978).

Development. No information.

Vocal array. Figure 3. Call and song not distinguished. Birds make a moaning growl perhaps best described as reminiscent of the drill and suction of a dentist. Other comparisons include "the note [is] somewhat like the bray of a donkey interpolated by a husky snore" (Lamb 1927: 68) and "the note is a series of choking cries coupled with a hissing, like escaping steam" (Anthony 1900: 249).

Phenology. Not studied.

Daily pattern. Calls only at night, with little or no moon. Calls begin about 45 min after sunset or are concurrent with moonset and last throughout the night. On Natividad I., no peak calling period. On dark nights during height of breeding season, calls

usually start and continue at similar rate (about 10–15 calls/min recorded on the colony) until cessation of calling (BSK). On nights with some moon, or late in breeding season, calls are less frequent. Normal interaction involves group of 4–6 birds vocalizing around burrow entrances, followed by fighting (see: Behavior: agonistic behavior, below).

Places of vocalizing. Birds call in air, from the ground, and in burrows. Rarely heard vocalizing from burrow during daylight, occasionally during moonlight. No information about calls at sea.

Social context and presumed functions. Not well known. See above.

NONVOCAL SOUNDS

None with a communicative function.

BEHAVIOR

LOCOMOTION

Walking, hopping, climbing, etc. Legs placed far back on body, and tarsi flattened; these are excellent features for swimming, but awkward for travel on land. Individuals shuffle along ground on tarsi. Use wings half open to help propel them in a run or over vegetation and other obstacles.

Flight. Flutters quickly and glides low over water (Harrison 1983). Stiff wing-beats, with short (rarely prolonged) glides (Howell and Webb 1995). Individuals bank and change direction regularly over water, rarely >20 m from sea surface. Speed estimated at 11–18 m/s, depending on wind (Spear and Ainley 1997b). Flies mostly across wind (Spear and Ainley 1997a).

Swimming and diving. Good swimmer. Paddles with feet on surface while dipping with bill for food. Dives from surface or from air just above surface. Uses wings folded at carpal joint to "fly" underwater, as Manx Shearwater does (Lockley 1942). Can reach depths of 52 m; average maximum dive depth is $21 \text{ m} \pm 11 \text{ SD}$ (n = 30); dives deeper during chick-

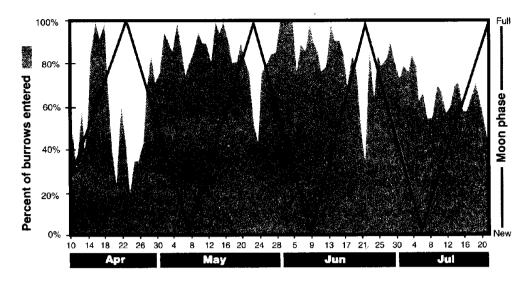


Figure 4. Percentage of Black-vented Shearwater burrows entered each night between 10 Apr and 22 Jul 1997. Data are from Natividad I. for 28 burrows with breeding adults; period extends from midincubation through fledging.

provisioning (average 24.3 m \pm 12.3 SD, n = 19) than during incubation (average 16.3 m \pm 4.2, n = 11; Keitt et al. 2000).

SELF-MAINTENANCE

Preening, head-scratching, stretching, bathing, anting, etc. Occasionally preens on land at colony. No observations, but probably preens on water in flocks before sunset, as Manx Shearwater does (Witherby et al. 1943). Juveniles stretch wings and practice flight on dark nights in front of burrows before fledging.

Sleeping, roosting, sunbathing. Behaviors mostly unreported. Some birds sleep on surface of colony at night with bill tucked under scapulars.

Daily time budget. At Natividad I., forms large rafts of up to 5,000 birds offshore prior to sunset, before coming ashore at the colony during breeding season. Rafts form 1–2 h before sunset and remain there until light level is low enough to allow individuals to come ashore. In 1997 on Natividad I., flocks began arriving on the water 10–140 min before sunset (average 66 ± 45.1 SD, n = 9 flocks). In 1998, birds arrived on average 123 min \pm 24 SD (n = 6) before sunset (Keitt 1998). Similar rafts of several hundred individuals reported offshore of San Benito and Guadalupe Is. at sunset (Everett 1988).

At Natividad I., radio-tagged individuals spent up to 5 h loafing offshore without feeding until moonset; then came ashore and attended burrow (Keitt 1998). Individuals active at colony from shortly after sunset to just before sunrise. If ambient light is less than –2.2 log lumens/m², not active above ground at colony (Keitt 1998). See also Predation, below.

Time budget at sea not known.

During breeding season, most burrows of breeding birds are entered every night except during periods

of bright moon (Fig. 4). Activity in burrows consists of incubation shift exchanges and feeding of chick.

AGONISTIC BEHAVIOR

Physical interactions. Adults fight above ground at night using bills (BSK). Presumably interactions are to defend territory around burrow. During group chorusing (see Sounds: vocalizations, above), 1 bird may chase ≥1 bird away from area; if an individual stands ground, fighting with bill ensues (BSK). Actual interaction lasts <20 s. Sex of individuals fighting not known, nor is frequency of interactions.

Communicative interactions. Primarily vocal; physical interactions not reported. Use of vocal communication is probably related to nocturnal behavior and inability to see other birds. In Manx Shearwater, vocalizations are thought to provide individual recognition, perhaps minimizing need for physical displays (Brooke 1990).

SPACING

Forms tightly packed rafts on water nearshore to breeding islands; rafts range in size from several hundred individuals to several thousand (Everett 1988, Keitt 1998).

On Natividad 1., density of breeding burrows averages 0.032 m⁻² \pm 0.0092 95% CI (n = 88) in low-density areas, 0.083 m⁻² \pm 0.0015 95% CI (n = 93) in high-density areas (Keitt 1998).

SEXUAL BEHAVIOR

Mating system and sex ratio. Little information. Presumably monogamous, like most other shearwaters (Warham 1990). Probably starts to breed at 5 yr of age (as Manx Shearwater does; Brooke 1990). No information on sex ratio.

Pair bond. No information. Extra-pair copulations. Not studied.

SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree of sociality. Highly gregarious and colonial at Natividad I. Possibly less so at other breeding sites, where densities are lower and other hole- and cavitynesting species are present. Forms flocks offshore of several hundred to several thousand individuals before arriving at colonies. Activity on land is poorly known because of nocturnal behavior, but individuals do sit in groups of 2–8 birds on surface near burrows (see Sounds: vocalizations, above).

Nonpredatory interspecific interactions. Burrows on Natividad I. apparently are occupied exclusively by Black-vented Shearwaters, so no interspecific interactions recorded among burrow-nesting birds. Western Gulls (Larus occidentalis) nest throughout Natividad I. colony. Little interaction between the 2 species, although Western Gulls may limit access to some burrows by nesting near the burrow entrance and physically inhibiting access to the burrow. Interspecific interactions not recorded at other colonies. At sea, regularly flocks with Sooty Shearwaters near colony when that species is present.

PREDATION

Kinds of predators. Avian predators include Peregrine Falcon (Falco peregrinus), Western Gull, and Common Raven (Corvus corax). Predation on adults by all 3 species observed on Natividad I. (BSK); juveniles also probably taken.

Feral cats kill large numbers of Black-vented Shearwaters on Natividad I. (BSK). Dogs (Canis familiaris) dig up burrows and kill adults and juveniles. Native deer mice (Peromyscus maniculatus) may depredate eggs, as occurs on other seabird islands with mice populations.

Response to predators. Burrow-nesting helps protect adults, eggs, and chicks from avian and some mammalian predators. Nocturnal activity patterns at the colony significantly limit overlap with activity of Western Gulls, thus reducing gull predation (Keitt 1998). Shearwaters are not active on colony surface during periods of daylight and bright moonlight corresponding to greater than -2.2 log lumens/m². Frequency of entering burrows is also diminished at these times (see Self-maintenance, above). Predation rate on individuals by Western Gulls on Natividad I. is greatest during daylight, reduced during moonlight, and minimal during light levels < -2.2 log lumens/ m². This species appears to have altered its behavior patterns to limit overlap with Western Gull, thus minimizing predation.

Nocturnal activity and lack of agility on the ground make this species particularly susceptible to nocturnal mammalian predators, such as cats. Black-vented Shearwaters have no defenses against these predators. Delong and Crossin (1968) hypothesized that the secretive behavior of the Black-vented Shearwater they observed on Natividad I. was a result of years of cat predation.

BREEDING

PHENOLOGY

Pair formation. No information.

Nest-building. Maintains burrows throughout breeding season. Digs new burrows probably Dec-Jan, before egg-laying. Artificial burrows that were placed on Natividad I. in last week of Dec 1996 were occupied the following breeding season, suggesting at least some burrow selection and perhaps nest-building occurs after late Dec (BSK).

On Negro Islet, off Guadalupe I., single birds began occupying burrows in late Nov (Jehl and Everett 1985), indicating that burrows were dug before this time.

First/only brood per season. Figure 5. Not well studied. On Natividad I. in 1997, egg-laying (estimated from hatch dates) began in third week of Mar, peaked 27 Mar, and lasted 2 wk. In 1998, egg-laying was initiated in first 3 wk of Apr, peaked 17 Apr, and lasted about 4 wk (Keitt 1998). In 1998, warm-water conditions (El Niño phenomenon) were prevalent, a condition that frequently causes reduced prey availability and poor reproductive success in seabirds (Schreiber and Schreiber 1984). The later egg dates and greater spread of laying in 1998 may have been a result of the El Niño conditions.

First eggs on offshore rocks near Guadalupe reported 5 Mar, with peak laying in early Apr through early Jun. This report corresponds to first chick date of 25 Apr (C. Hubbs in Jehl and Everett 1985).

On average, incubation lasts 49 d, and chicks fledge at 68 d of age (see Incubation, below, and Fledgling stage, below).

NEST SITE

Selection process. Not known. Does use artificial burrows (Keitt 1998).

Microhabitat; site characteristics. Digs burrows in sandy soil. On Natividad I., burrow densities are highest along bottom sides of drainages, perhaps because of soil depth and quality in these areas (on top of hills soil is blown away by wind and therefore substrate tends to be thin soil and rock).

On Natividad I., all nests are in burrows or modified crevices where individuals have excavated beyond natural crevice entrance. On offshore islets of Guadalupe I., all reported nests are in rocky crevices. On San Benito Is., uses both burrows and crevices. Crevice nests tend to have larger nest chambers, and frequently nest is visible from entrance (nest chamber rarely visible from entrance of burrows). Nest chamber is

frequently sandy; egg is not known to be laid on bare rock. Not known which nest type is preferred on these islands. When available, entrances are often constructed under vegetation, which provides structural support for burrow opening. See also Habitat, above.

NEST

Construction process. Excavates burrow using bill to break apart sand; then kicks sand out of burrow with feet. Sometimes extends crevice nest sites by digging, but usually makes no alterations to the structure.

Structure and composition matter. Burrows are simple, but almost always long enough that incubating adult is not visible from the opening. Usually 1 opening/nest and 1 nest chamber/burrow. Burrow is wide enough for 1 bird to pass; nest chamber is slightly larger, to allow for both birds. Nest chamber is frequently bare sand, but many also contain small amount of dried vegetation, primarily the introduced ice plant. Individuals readily use artificial burrows.

Dimensions. On Natividad I., burrows average 0.95 m long \pm 0.32 SD (range 0.25–1.75, n=68). Entrances averaged 10.3 cm high \pm 3.0 SD (n=76) and 21.7 cm wide \pm 4.9 SD (n=76). Reported to be shallow nests (Anthony 1896), but in 1997 many nest chambers were 1–2 m below surface, this depth perhaps a result of humans walking through the colony over a long period of time and crushing shallower burrows.

Microclimate. Nest chamber is more humid than ambient air in artificial burrows; not known if conditions are the same in natural burrows (BSK). On Natividad I., temperature in occupied burrows during incubation period averaged about 22.5°C in 3 burrows. Lowest temperatures occurred between 02:00 and 04:00 and averaged about 21°C; highest temperature, 12:00–14:00, averaged about 24°C. Ambient air temperature at this time averaged a low of 14°C between 02:00 and 04:00 and a high of 28°C between 12:00 and 14:00.

Maintenance or reuse of nests. On Natividad I., 7 of 18 artificial burrows occupied in 1997 were reused in 1998. All of these were used by the same birds in both years.

Nonbreeding nests. None known.

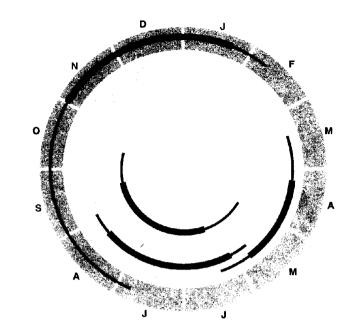
EGGS

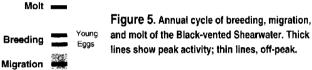
Shape. Elliptical ovate or elliptical oval (Bent 1922). Size. Average length 59.5 mm \pm 3.0 SD, width 40.4 \pm 1.1 SD (n = 10, Natividad I.; BSK). Bent (1922) reported average size of 60.9×41.2 mm (n = 38) and extremes of 69×40 , 60.5×43.5 , 56.6×41.4 , and 62.8×38.6 mm.

Mass. Average 51.5 g ± 4.0 SD (n = 13, Natividad I.; BSK).

Color. "Pure dead white" (Bent 1922). Can become stained from soil in nest later in incubation (BSK).

Surface texture. "Somewhat pitted but fairly smooth and not glossy" (Bent 1922: 81).





Eggshell thickness. Not reported.

Clutch size. One. Occasionally 2 eggs found in a burrow, but probably a result of egg-dumping by another female, or egg is from previous year (BSK).

Egg-laying. No information.

INCUBATION

Onset of broodiness and incubation in relation to laying. No information.

Incubation patch. Both sexes develop 1 brood patch on lower abdomen.

Incubation period. Not well studied. Observed incubation periods for 5 birds on Natividad I. were 42, 47, 50, 52, and 59 d. Exact laying dates, however, are not known for these data, so all are ± 3 d (BSK).

Parental behavior. No data, but male probably takes first incubation shift, as in most *Puffinus* shearwaters (Warham 1990). Both sexes incubate egg, presumably equally. Out of 9 incubation shifts of known length on Natividad I., 3 lasted 3 d, 4 lasted 4 d, and 2 lasted 5 d.

Hardiness of eggs against temperature stress; effect of egg neglect. Little information. Egg neglect occurs on Natividad I. regularly (BSK), but no information on frequency of occurrence. Eggs probably are able to withstand significant neglect, as with Manx Shearwater (Brooke 1990).

HATCHING

 ${\it Preliminary events and vocalizations}. Not known.$

Age (week)	Body mass (g)	Wing-chord (mm)	Culmen (mm)	Tarsus (mm)
1	$99 \pm 26 (8)$	29.3 ± 9.4 (3)	19.6 ± 8.4 (3)	20.9 ± 6.6 (6)
2	$189 \pm 43 (13)$	$39.2 \pm 5.6 (10)$	$25.0 \pm 5.4 (11)$	$28.6 \pm 4.9 (14)$
3	$245 \pm 49 (14)$	$52.5 \pm 8.5 (13)$	$27.1 \pm 3.0 (16)$	$34.1 \pm 5.3 (17)$
4	$298 \pm 64 (15)$	$79.2 \pm 12.1 (14)$	$30.1 \pm 3.6 (17)$	$38.9 \pm 6.1 (17)$
5	$329 \pm 59 (15)$	$108.8 \pm 12.6 (14)$	$32.2 \pm 4.7 (5)^{2}$	$41.8 \pm 7.3 (15)$
6	$368 \pm 93 (15)$	$137.2 \pm 13.1 (14)$	$33.9 \pm 5.2 (15)$	$42.6 \pm 7.5 (15)$
7	$403 \pm 94 (15)$	$162.1 \pm 13.3 (14)$	$34.5 \pm 5.3 (15)$	$43.2 \pm 7.6 (15)$
8	$402 \pm 79 (15)$	$183.4 \pm 15.4 (14)$	$35.1 \pm 6.0 (14)$	$43.3 \pm 7.6 (15)$
9	$399 \pm 10\hat{5} (1\hat{5})$	$206.1 \pm 13.1 (14)$	$34.8 \pm 7.0 (12)$	$43.3 \pm 8.1 (14)$
10	$377 \pm 74 \text{ (15)}^{'}$	$214.3 \pm 10.8 (14)$	No data	No data

Shell-breaking and emergence. Chicks emerge 2– 3 d after pipping (BSK).

YOUNG BIRDS

Condition at hatching. Altricial, ptilopaedic. Unable to thermoregulate. Mass at hatching not known; nestlings 4-7 d old weigh 90 g on average.

Growth and development. Chicks are smoke gray at hatching, developing white underparts in first few weeks. Gain mass at rate of about 75-125 g/wk for first 3 wk. Mass peaks at about 58 d old, at 0.9-1.15 times the average adult mass. Chick mass may decrease 10-20% in final 3 wk before fledging, at 68 d (Keitt 1998). Data on growth rate available only for 1997 and 1998 from Natividad I.; see Table 1.

PARENTAL CARE

Brooding. Little information. On Natividad I., 3 chicks observed daily during first 7 d after hatching: One was attended 4 d, and 2 were attended every other day for 6 d.

Feeding. Chicks receive partially digested regurgitated fish and other items from parent (see Food habits: diet, and Food habits: food selection and storage, above). Differences in male and female roles in feeding of chicks are not known. No data on size of meals, although regurgitations from adults on Natividad I. in 1998 averaged 43 g \pm 16.4 SD (n = 9). Regurgitations are thought to reflect meals for chicks. Not known to regurgitate stomach oil, as do procellariids that feed offshore. Chicks fed in typical procellariiform crossbill manner (Warham 1990). Figure 6 illustrates sequence of events during feeding of 5-wk-old chick. Two feeding events that were observed with an infrared camera lasted 6 and 8 min, respectively. The encounter was initiated by adult, followed by pecking at adult's bill by chick. Regurgitated food was delivered to chick in crossbill fashion several times during each event. After feeding, chick continued to peck at adult's bill, eventually stopping to rest.

Nest sanitation. Scorpions (order Scorpiones) frequently share burrow and nest chamber. Some

nests have many carabid beetles (order Coleoptera), and most have lice (taxonomy unknown) in nest chamber (BSK).

COOPERATIVE BREEDING

None reported.

BROOD PARASITISM

None reported.

FLEDGLING STAGE

Departure from nest. Young depart nest at average age 68.3 d \pm 3.7 SD (range 61–73, n = 15; BSK). Fledglings are independent of parents when they leave nest. Young exit burrows at night for several nights to exercise wings before fledging.

Growth. Chicks on Natividad I. in 1997 fledged with the following average measurements: mass $354 \text{ g} \pm 38.1 \text{ SD}$, tarsus $45.1 \text{ mm} \pm 2.0 \text{ SD}$, culmen 35.4 mm \pm 1.5 SD, wing 230.2 mm \pm 5.9 SD, tail 75.0 mm \pm 2.9 SD (n = 53).

IMMATURE STAGE

No information on immature birds once they leave the colony.

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY

Age at first breeding; intervals between breeding. No information on age at first breeding; probably similar to that of Manx Shearwater, which first breeds at 5 or 6 yr (Perrins et al. 1973). Little information on interval between breeding, but probably breeds annually like most shearwaters (Warham 1990).

Clutch. See Breeding: eggs, above.

Reproductive success. On Natividad I. in 1997, hatching success (percentage of eggs laid that hatched) 53% (n = 58 eggs), nestling success (percentage of chicks hatched that fledged) 69% (n = 28 chicks), and overall reproductive success (percentage of eggs laid

that fledged a chick) 36% (n = 58). Hatching success in 1998 was 47% (n = 36; Keitt 1998). Most common cause of chick mortality in these years appeared to be starvation as result of parental neglect.

Data on reproductive success not available from other islands.

Reproductive success observed for this species is on lower end of range reported for other *Puffinus* shearwaters. Manx Shearwater reproductive success ranges from 62 to 75% in most colonies, though only 43–64% on Rum I., Scotland (Lee and Haney 1996). Range for Wedge-tailed Shearwater reported as 47–80% (Byrd et al. 1983). El Niño conditions (high sea surface temperatures) were present at end of breeding season in 1997 and in 1998. Low food availability associated with El Niño conditions could explain the low reproductive success observed during these years (Schreiber and Schreiber 1984).

LIFE SPAN AND SURVIVORSHIP No information.

DISEASE AND BODY PARASITES No information.

CAUSES OF MORTALITY

Peregrine Falcons, Western Gulls, and Common Ravens all kill and eat adult and/or juvenile Blackvented Shearwaters. See Behavior: predation, above.

RANGE

No information.

POPULATION STATUS

Numbers. Populations on San Benito and Guadalupe Is. poorly known. Estimates for Guadalupe I. include 150 pairs in mid-1960s (Delong and Crossin 1968, based on nest surveys on Negro and Afuera Islets), 100-150 pairs in early 1970s on Negro Islet and 150+ pairs on Afuera Islet in 1968 (Jehl and Everett 1985). Counts of flocks on the water around Guadalupe I. and Negro and Afuera Islets yielded an estimate of 500-2,500 pairs in the region (Jehl and Everett 1985). This indicates that other colonies may exist as these numbers are too large to be accommodated on Afuera and Negro Islets alone. Estimates for San Benito Is. range from 150 pairs (Delong and Crossin 1968) to 250-500 pairs (Everett and Pitman 1993). Natividad I. is clearly the stronghold of this species. The most comprehensive population estimate for Natividad was from 1997: 76,570 pairs ± 18,411 SD (Keitt 1998). Keitt derived this number by estimating number of burrows in the colony and determining burrow occupancy with an infrared burrow camera. Briggs et al. (1987) estimated that 20,000-30,000 individuals may disperse to California waters in any given year.

Trends. No data available on colony sizes or on densities at sea to estimate trends. Anecdotal ob-







Figure 6. Sequence of events in feeding a 5-wk-old chick, observed on Natividad I. in 1998. Drawing by Carleton Eyster from sketches made in the field by Felipe Becerril Morales.

servations follow: The breeding population thought to be decreasing (Delong and Crossin 1968). Widespread mortality reported by many visitors to Natividad I. (Everett 1988). The enormous flocks of this species off Baja California reported in 1890s (Anthony 1896, Grinnell 1897) are no longer seen (Everett 1988).

On Natividad I., considerable mortality from cats. Keitt (1998) estimated mortality in the colony at 1,012 birds/mo \pm 340 SD in 1997, mostly as result of cat predation. A metabolic model used to estimate cat predation on this shearwater showed that 20 cats could eat 980 shearwaters/mo, leading to decrease in annual population growth by 4%; population is stable without cat predation (Keitt 1998).

POPULATION REGULATION

Does not appear to be limited at breeding colonies by habitat. Only 70% of burrows were occupied on Natividad I. in 1997; burrows do not appear to be at maximum density throughout the colony. Colonies on San Benito and offshore rocks of Guadalupe Is. are small and do not fill the abundant crevice habitat available on these islands. Competition with other burrowing seabirds may limit access to crevices on San Benito Is. and to a lesser degree on offshore rocks of Guadalupe I.

Decrease in burrow occupancy and attendance at Natividad during 1998 El Niño (Keitt 1998) suggests that food can be a limiting factor.

CONSERVATION AND MANAGEMENT

EFFECTS OF HUMAN ACTIVITY

Shooting and trapping. Humans resident on Natividad I. in early 1900s had large impact on this species. C. Lamb (1927: 68) reported, "The Japanese fishermen caught sacks of these birds, which they used as bait for crayfishes [lobster, Panulirus interruptus]." Egging apparently occurred on Natividad I. regularly up to 1970s. Although a limited amount of egging may still occur, the island residents maintain that they dislike the taste of shearwater eggs and satisfy their needs with Western Gull eggs, which are easier to collect (BSK).

Collisions with stationary/moving structures or objects. Attracted to light; will fly toward a light source. Collides with buildings, electric wires, and other objects in town on Natividad I., though extent of mortality not documented. Effects of lights and collisions with buildings and electric wires cause high mortality in Newell's Shearwater; effects on Black-vented Shearwaters probably significant as well (Telfer et al. 1987, Ainley et al. 1997).

Fishing nets. The effects of an increasing gill-net fishery near the breeding colonies on Natividad Is. and San Benito are not known. Potentially vulnerable to nets (Everett and Pitman 1993).

Degradation of habitat. All breeding islands have permanent human inhabitants. On Natividad I., effects of the town have been significant. Residents of Natividad report that the town was built on top of some of the densest nesting habitat on the island. The town occupies 285,000 m², about 11% of the colony area. In addition, there are 11 km of roads through the colony and a 30,000-m² dump. Using average burrow densities for the colony, it is estimated that development on the island has led to loss of 26,532 burrows, 15% of the total (Keitt 1998).

Because the Black-vented Shearwater is a coastal species, its distribution at sea overlaps with area of highest human use. Foraging habitat has possibly been degraded by gill-nets and marine pollution (Everett and Anderson 1991, Everett and Pitman 1993). The flocking behavior of this species makes it vulnerable to local oil spills.

Introduced animals. Cats have caused considerable mortality of Black-vented Shearwaters at all colonies. Cats are thought to have eradicated the colony on Guadalupe I. Cats are no longer present on San Benito Is., but they were reported in the past (Anthony 1925). Large numbers of birds are killed every month on Natividad I. by cats (see Behavior: predation, above). Removal of cats is a prime conservation goal.

Rabbits were released on San Benito Is. in early 1990s and rapidly multiplied. The same could happen on Natividad I., where residents sometimes keep rabbits for food. Feral rabbits compete for nesting burrows and destabilize the soil by overgrazing the vegetation (Ainley and Lewis 1974). Rats are not reported on any of the nesting islands, except Guadalupe. However, frequent supply trips to mainland towns are a possible vector for introduction of rats. Stopping the introduction of rats is a priority.

Large herbivores (goats, sheep, and burros) occur or occurred on all main breeding islands. On West San Benito I., burros crush Black-vented Shearwater nesting burrows. About 15,000 goats are feral on Guadalupe I., and they probably have reduced shearwater nesting habitat (Donlan et al. 1999). Goats and sheep were removed from Natividad I. in 1997; their effect on the shearwaters was unknown (Keitt 1998).

Chickens are present on Natividad I. and occasionally on San Benito Is. The possibility of the transmission of avian diseases via chickens is a concern.

Disturbance at nest and roost sites. Island residents on Natividad I. collect Western Gull eggs during the shearwater breeding season. Crushed burrows are a frequent result. Island residents also drive through the colony after dark, causing birds to become disoriented and sometimes collide with vehicles.

MANAGEMENT

Conservation status. Listed as Vulnerable by International Union for the Conservation of Nature (IUCN), primarily on the basis of the small number of breeding locations for this species. Offshore rocks of Guadalupe I. are in the Isla Guadalupe Special Biosphere Reserve, and Natividad I. is in the core area of the Vizcaino Biosphere Reserve. These designations do provide some measure of protection to the breeding colonies, but enforcement is minimal, as evidenced by problems with continued road-building and town expansion within the colony on Natividad I.

Areas Naturales Protegidas ("Natural Protected Areas") oversees the San Benito Is., and conservation actions on the islands are its responsibility.

Measures proposed and taken. An education program on Natividad I. was undertaken in 1997 by the Vizcaino Biosphere Reserve and the Island Conservation and Ecology Group, a binational nonprofit group dedicated to the conservation of seabird habitat. This work included setting up signs outlining restrictions on bringing introduced animals to the islands and designating certain areas of the island as having restricted access. Education programs in the local schools used games, videos, and field trips to raise awareness about this shearwater. Programs to remove introduced animals were begun in 1997. All goats and sheep on Natividad I. were removed in Oct 1997. Feral cats are scheduled to be trapped off the island in the year 2000. Efforts to limit dog

populations and stop further introductions are ongoing.

On San Benito Is., education programs are needed to bring awareness of seabird colonies to island residents. Signs, such as those on Natividad I., are needed.

Feral rabbits were removed from San Benito Is. in 1999 by the Island Conservation and Ecology Group.

Effectiveness of measures. Programs to remove introduced animals have been recently completed or are ongoing. To date, there is no information on the status of this shearwater after removals have taken place.

APPEARANCE

MOLTS AND PLUMAGES

See Figure 5.

Hatchlings. First downy plumage varies in color from light drab to pale smoke gray below (Bent 1922). Chicks are completely covered in gray down, which lightens during the first few weeks of development; throat and breast are paler gray.

Juvenal plumage. No information on timing or sequence of Prejuvenal molt. Juvenal plumage resembles adult (Definitive Basic) plumage (see below) though at fledging juveniles are darker, almost black in comparison to the worn plumage of adults. Loomis (1900: 360) observed, in what he thought were immature birds, "The white of the lower parts is also invaded by gray, the jugulum and throat being mottled, and in some cases the chin and fore breast. An extreme specimen is sparsely spotted on the abdomen and posterior portion of the breast. Some specimens display considerable white on the lower tail coverts."

Definitive Basic plumage. Number of molts between Juvenal and Definitive Basic plumages not known. Breeding adult Black-vented Shearwaters begin primary and contour feather molt concurrently with chick-hatching, in early May (Keitt et al. 2000). No molt was observed in Apr 1997. Primary and contour feather molt was first observed in first week of May 1997. Over 50% of birds were molting in last week of May. In mid-Jun, >95% of birds were molting, and they continued in heavy molt through Jul, when observations ceased. Molt began with inner primaries and proceeded sequentially outward (Keittet al. 2000). Loomis (1918) inspected molt in specimens collected off Point Pinos, CA, in 1907-1913. Keitt's observations agree with those of Loomis: Contour and primary molt observed in Jul, Aug, and Sep-some Sep birds having completed primary molt. Rectrix molt was observed only in Jan and Feb specimens. Mar and Apr specimens showed little to no molt.

Head is dark brown, rarely appearing blackish; sides of head and neck dusky, bleeding into white throat. Upperparts brown; variable dusky mottling on wing-coverts and flanks. Underparts mostly white but

the zones between dark and light are variable and dark smudges and diffuse specks of mottling can extend well into the white areas. Some birds have a partial or even complete breast band. Contour feathers of throat may be entirely dusky. Under tail-coverts are dark but extent of white intermingling near the vent is variable. Underwings are white with a narrow dark leading edge. Diagonal dusky smudge from the carpals to the humerals on the underwing is described as an "ulnar stripe" (Roberson 1996: 22). Some individuals entirely dusky underneath (Howell and Webb 1995).

BARE PARTS

Bill and gape. Bill dark gray, sooty. Iris. Dark brown.

Legs and feet. "Light yellowish, flesh-color" (Coues 1864: 140).

MEASUREMENTS

LINEAR

See Table 2. Males tend to be larger than females, though differences are not significant.

MASS

Average adult mass for breeding and nonbreeding birds from Natividad I.: $408 \text{ g} \pm 44 \text{ SD}$ (range 332–545, n = 258; Keitt 1998).

PRIORITIES FOR FUTURE RESEARCH

- 1. The population status in the San Benito Islands and on Guadalupe Island and its offshore rocks needs to be determined. In addition, information on dispersal between the colonies via extensive banding would help in understanding the importance of these smaller colonies to the overall productivity of this species.
- 2. Information on mortality and population trends on Natividad Island after cat removal will be important.
- 3. The causes and rates of mortality at sea, such as in gill-nets, deserve attention.
- 4. Comparative studies of the energetics between the coastal Black-vented Shearwater and the pelagic *Puffinus* shearwaters could prove interesting.
- 5. Distribution limits in the southern range of this species remain poorly known.

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	Male ¹	Female ¹	Sex unknown ²	Source ³
Culmen	37.3 ± 1.3 (34.9–39.4, 13) 37.5 (35.4–41.2, 30) 37.3 (34.8–39.5, 62)	36.6 ± 1.1 (34.4–37.9, 8) 36.9 (34.2–37.8, 19) 35.7 (33.3–38.5, 41)	$36.5 \pm 1.8 \ (32.1 - 41.3, 253)$	A B C
	37.3 (34.6-37.3, 62)	33.7 (33.3–36.3, 41)	36.8 ± 1.8 (33–39, 13)	Ď
Wing-chord	236.2 ± 6.0 (222–246, 14) 237 (213–251, 30) 244 (234–254, 62)	235.6 ± 6.5 (231–250, 10) 237 (214–246, 19) 243 (235–252, 41)	233 ± 5.8 (215–248, 260)	A B C
	244 (234-234, 62)	243 (233–232, 41)	240 ± 5.3 (231–252, 13)	D
Tail	75.8 ± 3.4 (71–80, 11) 78.4 (72.4–82.6, 30)	77.1 ± 1.7 (75–82, 8) 78.3 (74.7–81.4, 19)	74.2 ± 3.2 (62–81, 251)	A B C
	78 (74–84, 62)	79 (71–83, 41)	79.2 ± 2.9 (72–83, 13)	D
Toe ⁴	52 (49–55.8, 62)	51.4 (48–54.5, 41)	,	C
Tarsus	46.7 ± 0.9 (45.1–48.3, 14) 45.8 (43.6–48.1, 30) 43 (39.4–45.5, 62)	45.6 ± 1.2 (44.2–47.3, 10) 45.5 (43.2–47.9, 19) 42.3 (39.4–45.9, 41)	$46.2 \pm 1.3 \ (42.3-50.5, 258)$	A B C
	43 (37.4-43.3, 62)	42.3 (37.4-43.7, 41)	$45.1 \pm 1.6 (43-49, 13)$	Ď

¹Measurements from dead birds.

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²For data from Keitt 1998, measurements from live birds during breeding season, Natividad I.

³A = Keitt 1998; B = Murphy 1952; C = Loomis 1918; D = Bourne et al. 1988.

⁴Middle toe and claw.

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