

Wedge-tailed Shearwater *Puffinus pacificus*
Order PROCELLARIIFORMES Family PROCELLARIIDAE



Introduction

The Wedge-tailed Shearwater is a pelagic seabird of the tropical and subtropical Pacific and Indian Oceans. The wailing sounds that shearwaters make sitting in or near their burrows during the night have given rise to their Hawaiian name, which means “calling or moaning petrel.” Characteristically, this species nests on small islands, laying its single white egg in a burrow in the ground. It is a dusky brown bird with a musky odor to its feathers; white breast-feathers are visible in some forms. Wedge-tailed Shearwaters are polymorphic: There are dark, light, and intermediate forms. The light and dark morphs bear no relation to age, sex, or breeding status. In the air, the irregularly white undersides of the wings are apparent in birds with light plumage; so also is the wedge-shaped tail from which the species derives its name. The wings are long and thin; shearwaters are named for the way in which their motionless wings skim (shear) the water in gliding flight.

Shearwaters feed offshore, by “contact-dipping” with their long, slender bills. The placement of the legs far back on the body is adaptive to swimming underwater but, for the same reason, Wedge-tailed Shearwaters appear awkward on land, waddling rather than walking. They feed mainly on larval forms of fish such as goatfish and flying fish, and they feed mostly during the day in association with skipjack tuna and other predatory fish.

Wedge-tailed Shearwaters breed from Madagascar in the western Indian Ocean to the Revillagigedo Is. in the eastern Pacific, off Mexico. Males and females share the digging or renovation of the burrow and mate in or near it. After mating, both members of the pair return to sea for up to 4 weeks. This prelaying exodus allows the female to feed while developing the egg. Egg-laying is synchronous in Wedge-tailed Shearwater colonies; both members of the pair share the long incubation spells. The egg is relatively large and the incubation period long. Shearwater nestlings grow to exceed the body mass of the adults, but they are deserted by the parents several weeks before fledging.

The Wedge-tailed Shearwater is long-lived and is one of the most abundant species of seabirds in the Hawaiian Islands.

Distinguishing Characteristics

Largest of tropical shearwaters: overall length about 43 cm, body mass 390 g. Slender body; long wedge-shaped tail; hooked bill. Polymorphic. Light-morph birds grayish brown above with white underparts except for dark edges to wings and dark undertail-coverts. Dark slate-colored bill and flesh-colored legs. Dark morphs are uniformly sooty brown.

Sexes indistinguishable; female can be identified shortly before and after laying by the dilated, swollen, and often discolored cloaca ([Gross et al. 1963](#), [Shallenberger 1973](#)). Immature birds resemble adults in appearance.

In North Pacific, light morphs predominate except on Revillagigedo Is. (18°N; see [Fig. 1](#)), where only 1 in 600 birds is a light morph ([Jehl and Parkes 1982](#)). South of latitude 10°N in Pacific Ocean, almost all birds are dark morphs. Most birds in Australian waters and in Indian Ocean are dark ([Watson et al. 1963](#), [Serventy et al. 1971](#)).

Dark morphs may be distinguished from Flesh-footed Shearwater (*Puffinus carneipes*) in Mexican waters by more buoyant flight with bowed wings angled back at carpals, and a proportionately longer tail ([Howell and Webb 1995](#)). Darker bill less conspicuous than large pink bill of Flesh-footed Shearwater. In the Hawaiian Is., Newell's Shearwaters (*Puffinus auricularis newelli*) have glossy black upperparts contrasting sharply with pure white underparts. Christmas Shearwaters (*Puffinus nativitatis*) are uniformly sooty-brown, including bills, legs and feet, with short round tails.

Distribution

The Americas

Breeding Range

Breeds on San Benedicto I. in Revillagigedo Is. off west coast of Mexico ([Everett and Anderson 1991](#))—the easternmost breeding site of this species.

Nonbreeding (Marine) Range

In e. Pacific, both light and dark morphs are abundant in the eastward-flowing Equatorial Countercurrent (latitude 4–9°N). Seldom seen in se. Pacific west of Peru Current (longitude 90°W) ([Au and Pitman 1988](#)). Two photo records for California: off Monterey, 31 Aug 1986 (light morph) and inland at Salton Sea, 31 Jul 1988 (dark morph).

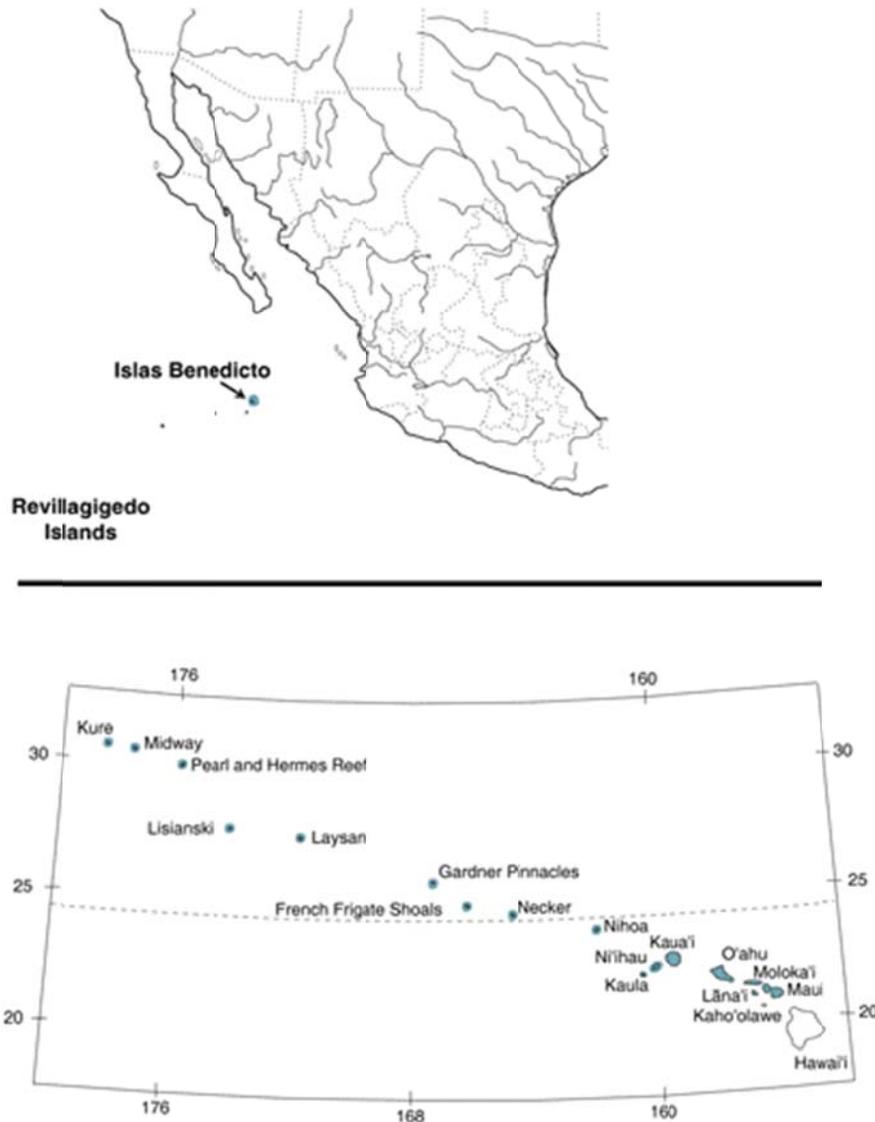


Figure 1. Breeding distribution of the Wedge-tailed Shearwater off the west coast of Mexico and in the Hawaiian Islands.

Outside The Americas

Breeding Range

Breeds extensively in Hawaiian Archipelago from Kure I. in north to offshore islets of Maui I. in south ([Harrison 1990](#)). Central Pacific breeding sites also include Johnston Atoll and Christmas I. (in Line Is.). In North Pacific, breeds on Pescadores (westernmost breeding area), Bonin Is., Volcano Is., Marshall Is., and Caroline Is. ([King 1967](#), [Robinson 1982](#)). Breeds on islands throughout South Pacific as far south as Lord Howe I., and as far east as Pitcairn I. ([King 1967](#)). Also breeds off eastern and western coasts of Australia ([Serventy et al. 1971](#), [van Tets and Fullager 1984](#)). Breeding range in Indian Ocean extends from westernmost breeding site off west coast of Madagascar ([Appert 1965](#)), to Seychelles in north, Cocos Is. in east, and Reunion I. in south ([Watson et al. 1963](#)).

Nonbreeding (Marine) Range

In Pacific Ocean, marine range only slightly larger than breeding range: northernmost sighting, 35°26'N, 164°17'W (record of dark morph from Japan presumed to have been carried north by a typhoon; [Ezaki et al. 1993](#)). Reported from China ([Melville 1984](#)). Southernmost sightings from Cook Strait, New Zealand ([King 1974](#), [Jenkins 1979](#)). Sightings from Easter I. (26°S, 109°W) and Bismarck Archipelago (4°S, 150°E; [King 1967](#)).

In Indian Ocean, seen near Amsterdam and St. Paul Is. in south and in Bay of Bengal in north ([Tuck 1980](#)). Also in South African waters and Mozambique Channel ([Sinclair 1978](#), [Batchelor 1980](#)). Pale morph in Red Sea probably not from Indian Ocean population ([Bezzel 1987](#)).

Historical Changes

Evidence for former large concentrations in main Hawaiian Is., but at present few nest there.

Fossil History

Oldest shearwater fossil is of *Puffinus raemdonkii* from Oligocene, in Belgium ([Warham 1990](#)). Most modern species had evolved by mid-Miocene. *P. pacificus* is close to one of the more ancestral lines of shearwaters ([Austin 1996](#)). A Pleistocene fossil of a bird very similar to Wedge-tailed Shearwater, from St. Helena I., and an early Pliocene fossil from N. Carolina ([Olson 1985](#)) suggest that the species may once have been present in Atlantic Ocean. In Hawaiian Archipelago, Wedge-tailed Shearwater bones have been found at fossil sites on the main islands ([Olson and James 1982](#)).

Systematics



Figure 2. Two Wedge-tailed Shearwaters at Popoia Island, O'ahu. The individual on the left is a dark morph; the one on the right is a light morph. Photo by KDH.

“Discovered” in Society Is. (South Pacific) during Captain James Cook’s first voyage ([Oliver 1955](#)). Known by variety of local names throughout Pacific Ocean, Australia, and Indian Ocean. Much taxonomic confusion about this species ([Shallenberger 1973](#)).

Geographic Variation; Subspecies

Wedge-tailed Shearwater is polymorphic: light morphs, dark morphs, and gradations of intermediate morphs have been described ([Murphy 1951](#)). Difference is seen largely as absence or presence of white underparts. Although all gradations of color may occur at any geographic site ([Fig. 2](#)), there are also marked geographic variations. Dark morphs are relatively rare in North Pacific; in Indian Ocean and South Pacific, they predominate ([King 1967](#)).

No subspecies recognized by Jouanin and Mouglin ([1979](#)), but 2 subspecies recognized by Murphy ([1951](#)): *Puffinus pacificus pacificus* (from Kermadec Is., Norfolk I., and Kandavu I. in South Pacific), and *P. p. chlororhynchus* (elsewhere), said to have more powerful bill and longer wings and tail. This distinction has been disputed ([Oliver 1955](#)). Type specimen for *P. p. pacificus* is from Kermadec Is.; it represents only dark morphs ([Murphy 1951](#)).

Related Species

Closest relative is Buller's Shearwater (*Puffinus bulleri*; [Austin 1996](#)). Close resemblance between Buller's Shearwater and light-morph Wedge-tailed Shearwater, but upper surface of Buller's Shearwater is more gray, with obvious dark M across wing ([Oliver 1955](#)). The 2 species form the subgenus *Thyellodroma* ([Austin 1996](#)).

Migration

Nature Of Migration In The Species

Most birds leave breeding grounds for open ocean. Evidence of small resident population that remains at breeding colony outside breeding season in Phoenix Is., central Pacific Ocean ([King 1974](#)). Occasional sightings in Hawaiian Is. and visits to burrows on Christmas I. (central Pacific; there are no shearwaters on Christmas I. in Indian Ocean) in Dec suggest that birds in some populations are not completely absent outside breeding season ([Schreiber and Ashmole 1970](#), [Mull 1971](#)). There may be little migration in the more tropical Pacific populations ([King 1974](#)).

Timing And Routes Of Migration

Difficult to document migration in pelagic seabirds, but seasonal movements of birds provide evidence for migration, particularly in Pacific, where relative movements of the more northern light morphs and southern dark morphs allow identification of populations.

Breeders (70–90% dark morphs) are present on San Benedicto I. in Revillagigedo Is., Mexico, Mar–Oct; nonbreeders (light morphs outnumber dark morphs) are present in marine waters off coast of s. Mexico (north to s. Baja) primarily Nov–Jun, less commonly Jul–Oct ([Howell and Webb 1995](#)).

In e. Pacific, light and dark morphs are found in roughly same area, but they reach their highest densities at different times: light is most abundant Oct–Feb; dark, Jun–Sep. Eastern Pacific is probably wintering “grounds” for light morphs from Hawaiian Is., which migrate there along Equatorial Countercurrent and return via North Equatorial Current (north of 9°N) ([King 1974](#)). Hawaiian birds would have to travel south to Equatorial Countercurrent after breeding season, and then east to coast of Central America ([King 1974](#)). Mostly absent from Hawaiian Is. in Dec, but rare sightings during annual Christmas Bird Count on O'ahu I.

In central Pacific Ocean, dark morphs move north with northward movement of warm water in summer. Northward penetration of dark morphs begins in Apr, peaking in Jul and Aug, when they occur almost as far north as light morphs. Almost no dark morphs occur north of 10°N from Dec to Feb. In central Pacific, distribution of light morphs at sea is tied to breeding cycles of birds in Hawaiian Is. and Johnston Atoll. In winter, abundance of light morphs is lowest; in Feb, light morphs (see [Fig. 5](#)) are almost completely absent from central Pacific north of 10°N. Birds reenter the area in Mar, and from Apr to Nov maximal densities are recorded within 80–160 km of breeding islands. Thus, light morphs in central Pacific are breeders; dark morphs are a nonbreeding (wintering) population ([King 1974](#)). Light morphs peak in May or Jun.

A light morph that had been banded on Johnston Atoll on 19 Sep 1963 was found in Cook Strait, New Zealand, on 8 Nov 1985 ([King 1974](#), [Jenkins 1979](#)); suggests that other migratory pathways may involve central Pacific Ocean birds, but this could also represent merely an accidental presence in the area.

Migratory Behavior

From Sep to Nov, large flocks gather offshore before migration near Hawaiian Is. ([King 1974](#)); rafts of up to 700 birds.

Control And Physiology

Unknown.

Habitat



Figure 3. Breeding habitat of Wedge-tailed Shearwater in Hawaii

Breeding Range

Typically low, flat islands and sand spits with little or no vegetation. Integrity of the burrow demands either firm soil or some vegetation to hold soil together. Soils may be largely sand or of volcanic origin. Uses slopes of extinct volcanoes and old volcanic craters in main Hawaiian Is. ([Fig. 3](#)). Usually no tall woody plants in nesting areas; these would impair flight paths of birds to and from nesting burrows (see Behavior: locomotion, below), but grass can be quite long and dense in vicinity of burrow; in Australia, nests under forest. Breeding-site distribution correlated with ocean surface isotherm of 20°C for coolest months of year; no breeding sites at isotherms below 20°C ([Murphy 1951](#)).

Spring And Fall Migration

Migratory habitat is the ocean surface and air above.

Marine Range

Open ocean of tropics and subtropics. In Pacific, most abundant at seawater salinities of 34.6–34.9 ppt (parts per thousand); not seen at salinities <32.6 or >36.54 ppt ([King 1974](#)). Lowest sea temperature at which species occurs is 15°C; highest 33°C; most abundant at sea surface temperature of 26°C, within vicinity of equatorial currents ([King 1974](#)).

Food Habits

Feeding

Main Foods Taken

In Pacific Ocean, mostly larval forms of goatfishes (Mullidae), mackerel scad (Carangidae), flying fish (Exocoetidae), squirrelfish (Holocentridae), and flying squid (Ommastrephidae) are driven to surface by fish schools ([Harrison 1990](#)). Compared with birds on Christmas I., Hawaiian birds consume more fish than squid, and fewer flying fish, substituting goatfish and mackerel scad ([Harrison and Seki 1987](#)).

Microhabitat For Foraging

Surface feeder ([Brooke 1990](#)). Forages below ocean surface and in air close to surface. Offshore feeder; feeds within 80 km of Hawaiian Is. ([Harrison 1984](#)). Birds banded on O‘ahu are found in all directions, but within 160 km of island. During breeding season, birds banded on Johnston Atoll were recovered at sea within 480 km of island to southwest or northwest, with exception of 1 bird seen 2,000 km southeast of Johnston Atoll ([King 1974](#)). See also Distribution: the Americas, above.

Food Capture And Consumption

Most frequently observed feeding method is contact-dipping ([Ashmole and Ashmole 1967](#)): Bird flies close to surface and plunges head and neck down several inches into water. After catching a fish (7–8 cm long), bird swallows it in midflight with slight upward flip of head ([Gould 1967](#)). Dipping minimizes risk of being eaten by predatory tuna, sharks, or billfish ([Harrison and Seki 1987](#)).

“Feeding on the surface” is the next-most common feeding technique; usually executed from sitting position. Air-dipping (plucking flying fish from midair) and air-diving are also used. Observed taking flying fish in sw. Pacific just as fish return to water; bird lowers tail and spreads tail-feathers to reduce stall speed ([Jenkins 1979](#)). Follows boats discharging offal; prefers fish offal to fat ([Wood 1993](#)). Voracious, noisy, and aggressive when following a boat, feeding off offal, approaching as close as 4 m. Scavenging techniques include surface-seizing (grasps food from “sitting” position), surface-plunging (belly-flops onto water using momentum to catch food), and contact-dipping (pecks food from just below surface while in flight).

Very maneuverable while feeding ([Wood 1993](#)). Little evidence for swimming underwater in spite of compact plumage, compressed tarsi, and high specific gravity—all adaptations to swimming underwater. Of 5 species of Australian shearwaters (Wedge-tailed, Flesh-footed, Short-tailed [*P. tenuirostris*], Sooty [*P. griseus*], and Fluttering [*P. gavia*]), Wedge-tailed Shearwater has the least streamlined tarsometatarsi, correlating with absence of shallow diving or pursuit-diving in its feeding repertoire ([Wood 1993](#)). Nocturnal feeding recorded;

only contact-dipping seen at night ([Gould 1967](#)). Observed feeding under full moon between 23:30 and 23:45. Reduced colony occupation on moonlit nights may be correlated with nocturnal feeding ([Shallenberger 1973](#)).

In the Pacific, usually (93.4% of the time) feeds in flocks in association with other species of birds and in conjunction with skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*), dolphinfish (*Coryphæna* spp.), and other predatory fish ([King 1974](#)). Feeding flock of 150 shearwaters seen off San Benedicto I. in Revillagigedo Is. ([Jehl and Parkes 1982](#)). Since tuna feed primarily during day, so do shearwaters. Feeding flocks of Wedge-tailed Shearwater mixed with Townsend's Shearwaters (*Puffinus auricularis*) occur off Mexico ([Warham 1990](#)). Black Terns (*Chlidonias niger*) and Sooty Terns (*Sterna fuscata*) flock with Wedge-tailed Shearwaters over schools of skipjack tuna and porpoises in Gulf of Panama ([Harrison 1984](#)). In central and North Pacific feeds especially with Sooty Terns; conspicuous behavior of the latter may help shearwaters find food ([King 1974](#)). Also associates with Brown Noddies (*Anous stolidus*), Red-footed (*Sula sula*) and Brown (*S. leucogaster*) boobies, and Christmas Shearwaters (*Puffinus nativitatis*; [Harrison and Seki 1987](#)). Strong association with boobies and jaegers in feeding flocks in e. Pacific ([Au and Pitman 1988](#)). Much overlap between diets of Sooty Tern, skipjack tuna, and Wedge-tailed Shearwater. Flocks of birds and schools of fish often associate with cetaceans ([Fefer et al. 1984](#)). In e. Pacific, between 5° and 30°N, 43–53% of bird flocks associate with porpoises—mainly spotted (*Stenella longirostris*) and spinner (*S. attenuata*) dolphins. Bird flocks consist mainly of boobies (41.7%), Wedge-tailed Shearwaters (31.4%), and jaegers (12.8%). Farther south (5°N–12°S) and in central Pacific, <8% of flocks are in association with dolphins ([Au and Pitman 1986](#)). In Pacific, Wedge-tailed Shearwaters sit on water in small rafts after feeding ([King 1974](#), [Au and Pitman 1986](#)).

Diet

Major Food Items

In Hawaiian waters, by volume, 66% of prey are fish, 28% squid, and 1% crustaceans ([Harrison et al. 1983](#)). Diet known mainly for breeding season; only then are birds accessible. Dietary information derived mainly from studies in Hawaiian Archipelago.

Quantitative Analysis

Goatfishes are the most frequently taken prey; they constitute 17.6% by volume of stomach content ($n = 233$ birds; [Harrison et al. 1983](#)). Mackerel scad make up 25.2% of volume, flying squid 21.8%, and unidentified squid 6.4%. Average length of prey is 57 mm ($n = 212$ prey items), but food items ranged from a 4-mm sea strider, a marine insect (*Halobates seoiceus*), to a 145 mm mackerel (*Decapteous macrosoma*). Mean length of ommastrephid squid is 63 mm and of goatfishes 54 mm. Within Hawaiian Is., there are differences in selection of food items between islands and also between seasons ([Harrison et al. 1983](#)). At Midway Is., squid are important foods in spring, summer, and fall; on Laysan I., squid replaced by carangids in summer.

Food Selection And Storage

Food may be partly or completely digested by the time bird returns to colony. Stomach may contain 10–50 squid beaks, 2–3 mm long, occasionally as long as 10 mm. Squid and fish eye lenses, fish backbones, some algae, pieces of terrestrial vegetation, plastic debris, and stomach oil have been found in stomach ([Shallenberger 1973](#)). Stomach oil represents storage of energy and possibly other nutrients (see following section); it is similar in composition to dietary lipid: lots of triglycerides and cholesterol ([Cheah and Hansen 1970](#)).

Nutrition And Energetics

Composition of most food items for Hawaiian birds is known in terms of their energy, water, and ash content. Energy content of the 3 highest-ranking prey species (goatfishes, mackerel scad, and flying squid) varies from 3.4 to 4.8 kJ/g ([Pettit et al. 1984b](#)).

Energy requirements of population (3,500 breeders, 6,790 nonbreeders) at French Frigate Shoals in Northwestern Hawaiian Is. estimated to be 843.5 x 106 kJ in total over breeding season (200 d; [Pettit et al. 1984b](#)). From this figure and the energy content of the types of prey consumed, estimated that food consumption of entire population was 189.6 metric tons over breeding season. Fefer et al. (1984) extended this analysis to include the Wedge-tailed Shearwater population throughout Northwestern Hawaiian Is. (1,537,647 individuals), arriving at an estimate of 35,440 metric tons of food. Using a simpler estimate based on “existence metabolism,” Whittow ([1984a](#)) calculated that annual total energy requirement of adult population (1,590,500) in Northwestern Hawaiian Is. could be met by consumption of 48,186 metric tons of food. On basis of feeding experiments on captive birds (J. L. Sincock, R. Sincock and G. V. Byrd pers. comm.), it has been estimated that 31.622 kg squid would sustain 1 shearwater for 1 yr.

Daily energy expenditure (613.7 kJ/d) of free-ranging foraging birds at French Frigate Shoals ([Ellis et al. 1983](#), [Ellis 1984](#)) is 4.8 times the resting metabolic rate (see Metabolism and temperature regulation, below). Energy content of stomach oil is 39.3 kJ/g ([Pettit et al. 1984b](#)). Thick-walled intestine is 50 cm long; this is short by procellariiform standards, perhaps correlated with the relatively scarce food supply of tropical waters and a low rate of acquisition and digestion of food ([Kuroda 1986](#)).

Metabolism And Temperature Regulation

At French Frigate Shoals, mean resting metabolism per bird measured at air temperature of 28.9°C indoors was 128.4 kJ/d for 4 adult birds weighing, on average, 337.8 g ± 4.0 SD ([Pettit et al. 1985](#)). This metabolic rate was only 86% of predicted value for birds of this size. In a more extensive laboratory study ([Whittow et al. 1987](#)), resting metabolic rate measured in birds known to be within their thermoneutral zone (range of air temperature at which metabolic rate is constant) confirmed that this metabolic rate is relatively low.

Mean rectal temperature of 62 incubating adults removed temporarily from their burrows on Mānana I., an offshore island of O‘ahu, HI, was 37.8°C ± 0.8 SD during day; burrow air temperature was 28.1°C ([Whittow et al. 1987](#)). Stomach temperature (37.7°C ± 0.6 SD, *n* = 30) was similar. Average body temperature for Procellariiformes is 38.8°C ([Warham 1971](#)). At Midway Is., where surface-nesting is common, mean body temperature is higher: 39.5°C during day and 37.7°C at night ([Howell and Bartholomew 1961](#)). On Laysan I. in Northwestern Hawaiian Is., mean body temperature of birds that were not incubating, measured in the evening, was 39.0°C; lower in birds asleep (38.2°C), and higher (39.7°C) in birds active before measurement was taken ([Udvardy 1963](#)). Body temperature of resting, awake adults that were not incubating, within their thermoneutral zone, in the laboratory, was 39.3°C ± 0.7 SD (*n* = 13; [Whittow et al. 1987](#)). Mean temperature of foot webs was 33.6°C when air temperature was approximately 27°C at Midway Is. ([Howell and Bartholomew 1961](#)).

In response to exposure to cold, metabolic heat production increases by as much as 183% as a result of shivering ([Whittow et al. 1987](#)). At high air temperatures, birds pant at rates as high as 260 breaths/min, but shearwaters do not gular-flutter ([Whittow et al. 1987](#)). Under optimal conditions, evaporative heat loss can

exceed metabolic heat production during heat exposure. A well-developed network of veins (rete mirabile ophthalmicum) may drain cool blood from evaporating surfaces in airway and cornea of eye and cool arterial blood supply to brain by countercurrent heat exchange ([Pettit et al. 1981](#)). Physiological responses of adults and fledglings to heat and cold are indistinguishable.

Thermal conditions are most demanding during breeding season. These conditions are mitigated by the burrow, which provides protection against solar radiation, rain, and wind ([Whittow 1979](#), [Whittow et al. 1992](#)). In the old volcanic crater on Mānana I. off O‘ahu, black-bulb temperatures of 50°C recorded, and ground surface temperatures are as high as 52°C; air temperatures are as high as 38°C during day and as low as 25°C at night ([Shallenberger 1973](#), [Whittow et al. 1982](#)).

Drinking, Pellet-Casting, And Defecation

Little information. Never observed to drink. Derives some water from food: 3 main prey items (goatfishes, mackerel scad, and flying squid) consist of 76.0–78.8% water ([Pettit et al. 1984b](#)). Metabolism also produces water ([Grant and Whittow 1983](#)). Body water represents 65% of body mass ([Ellis et al. 1983](#)). See also Breeding: parental care, below.

Sounds

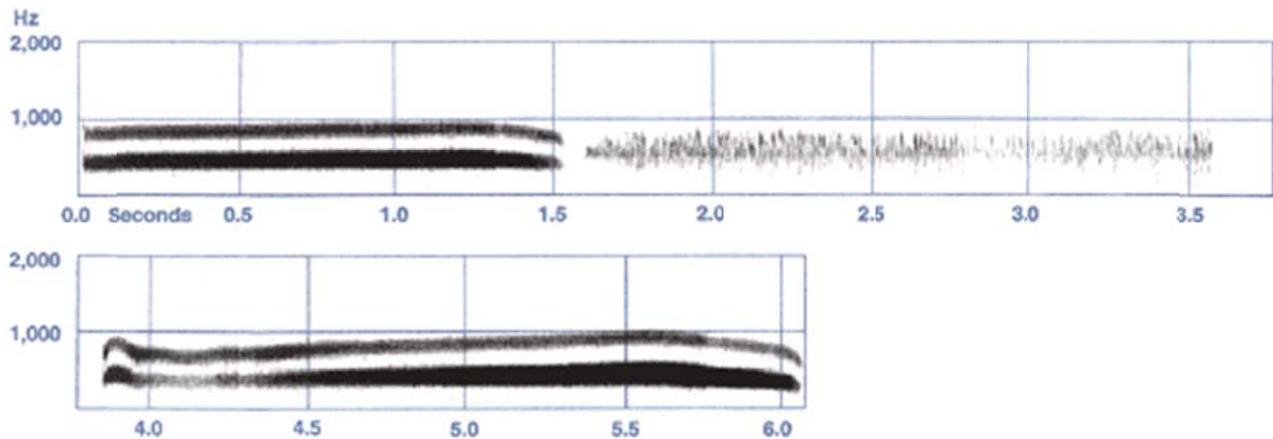


Figure 4. Wedge-tailed Shearwater vocalizations

Vocalizations

Development

Vocalizing begins at least 48 h before eggs hatch. At 2–5 d, chirps are simple cries; sound volume increases during first week after hatching. At nestling age of 10–12 d, chirp gradually changes to moaning of adults, calls are longer, and an inhalatory component appears. Calls in response to feeding or to any disturbance. Feeding call consists of 3-part chirp (2 frequency peaks) that lasts 0.22–0.35 s. Frequency peaks at 3–8 kHz. Maximal continuous call rate during food-begging is 65 calls/min. Uses longer calls when defending burrow ([Shallenberger 1973](#), [1984](#), [Warham 1996](#)).

Vocal Array

[Figure 4](#) . Birds moan while both inhaling (*OOO*) and exhaling (*err*), producing a basic 2-part call that is repeated. Deep growl made by exhalation alternates with shorter and higher snarl during inhalation. Throat and gular pouch expand during expiratory call ([Oliver 1955](#), [Serventy et al. 1971](#), [Shallenberger 1973](#)). In anesthetized birds, more sound is produced when lung deflates than when air is blown into lungs ([Shallenberger 1973](#)). Call lasts 1.29 s on average (range 1.13–1.47, $n = 5$). Starts at 279 Hz, peaks at 419 Hz, and ends at 297 Hz ([Gross et al. 1963](#)). Warham ([1996](#)) reports spectrogram of duet by pair of birds in burrow. Louder call is composed of 1 long (1.5 s) and 1 short note with harmonics; quieter call consists of shorter syllables with many harmonics. An alarm call is characterized by sudden onset, high pitch, and many harmonics.

Phenology

See Breeding: phenology, below.

Daily Pattern

Chorus of sound maintained throughout night, but level peaks after sunset and before sunrise. Calls are more intense and last longer at night than during day ([Shallenberger 1973](#), [1984](#)).

Places Of Vocalizing

On the ground or in burrows. Never heard in a lighted area (at night), at sea, or in flight ([Gross et al. 1963](#)). However, on 4 occasions birds were observed to “wail” in flight, in Kermadec Is. ([Crockett 1975](#)).

Repertoire And Delivery Of Songs

See above.

Social Context And Presumed Functions

Both birds call while allopreening. Series of short calls is common during courtship. Calls cease during initial part of copulation. Defense of burrow is accompanied by high-intensity version of basic 2-part call (see above). Male calls are longer and louder than those of female. Calls continue during combat, but they are more rapid after physical contact has been made. Vocal recognition between parents and young and between parents ([Shallenberger 1973](#), [1984](#)).

Nonvocal Sounds

No information.

Behavior

Locomotion

Walking, Hopping, Climbing, Etc

On land, advances by short runs ([Munro 1967](#)). Because of posterior placement of legs, adopts forward-tipped posture and sits on tarsi. This posture and shuffling gait are very effective for moving through grass. Uses bill and wings when scaling rocky surfaces ([Shallenberger 1973](#)). Never observed to hop.

Flight

Wedge-tailed Shearwater is the most aerial species of the genus *Puffinus*; relatively low wing-loading ([Warham 1996](#)). Proficient glider, perhaps helped by its wedge-shaped tail. Anatomical adaptations associated with gliding flight include short, slender scapula, weakly developed clavicle, short sternum, and narrow pelvis with large sacral holes ([Kuroda 1954](#)). Uses a modified dynamic soaring technique in flight, taking advantage of differentials in wind speed at different elevations above waves. Flight similar to that of albatross (*Diomedea* spp.; [Whittow 1993](#)), but shearwaters flap more ([Gross et al. 1963](#)). Flight alternates between gliding on rigidly outstretched wings and several rapid, stiff wing-beats ([Watson et al. 1963](#)). Wrists are held slightly bent. In moderate winds, remains horizontal. At higher wind speeds, arcs and banks more steeply. Seldom appears above horizon ([King 1967](#)); usually flies not >10 m above water ([King 1974](#)).

Takeoff preceded by partial wing extension and sometimes wing-flapping. Can take off from level ground in still air, but needs room to run and to fly at low altitude while gathering speed. Often gathers in open areas for morning takeoff. Homing birds fly several circuits before alighting in colony, and often take off again and repeat their flight pattern. Flies along approach path 0.6–3.1 m above ground at low speed; return path is higher and faster (9.2 m/s). On approach path, legs are dropped and wings partly extended. Approach path is oriented into wind ([Shallenberger 1973](#)).

Swimming And Diving

Shearwaters use wings and feet for propulsion underwater. Leg movements used for swimming are similar to those used for burrow excavation (see Breeding: nest, below).

Self-Maintenance

Preening, Head-Scratching, Stretching, Bathing, Anting, Etc

Preening is most common just after landing and immediately after copulation. Always includes scapulars and breast-feathers under each wing. Frequently supplemented by head-scratching with foot positioned under wing. Extensive preening follows defecation after prolonged incubation. Preening often preceded by rapid head and body shake that fluffs feathers ([Shallenberger 1973](#)).

Four distinct stretch postures: (1) Before takeoff, stands, fully extends wings, and briefly flaps. (2) After prolonged incubation, lowers head and partly extends wings; then often preens extensively. (3) Birds in pairs or groups frequently extend one wing laterally and tip their bodies to opposite side; common among birds that have recently landed or those that have been incubating for a long time. (4) Tips to one side but does not extend wing; this posture is never seen in lone birds ([Shallenberger 1973](#)).

Sleeping, Roosting, Sunbathing

Sleeps intermittently during night. Pairs of birds often sleep next to each other. Lightly sleeping birds retract neck and close eyes; birds with heads tucked under wing are in deeper sleep ([Shallenberger 1973](#)). Does not sunbathe.

Daily Time Budget

Little known about daily activity patterns at sea. Usually returns to breeding colony after sunset and leaves before sunrise. Activity in colony is greatest 3–4 h after sunset and 1.0–1.5 h before sunrise. In Apr and May in Hawaiian Is., incoming flights build up as early as 17:00. Fly in later in Jun and Jul than in Apr and May.

Incoming birds gather in large flying masses to east of Mānana I. off O'ahu before flying over the colony. Do not form rafts on surface of water in vicinity of this colony. On Mānana I., where there are no terrestrial predators, shearwaters are common over the colony and on the ground in daylight, before egg-laying. After eggs are laid, birds on Mānana I. are more strictly nocturnal, but not completely so. Incoming flights are reduced in moonlight, and number of birds on surface of ground is greatest when there is little moonlight. During day, remains on ground longer if there is shade ([Shallenberger 1973](#)). At Midway Is., strictly nocturnal: First birds seen in colony 15 min after sunset. All birds leave by 30 min before sunrise.

Agonistic Behavior

Physical Interactions

Birds that enter wrong burrow are vigorously ousted; attack is accompanied by loud yowls and violent flapping of wings ([Gross et al. 1963](#)). Birds fight, using only beak, in contested burrow chambers ([Nelson 1979](#)). Ejection of stomach oil is rare ([Shallenberger 1973](#)).

Communicative Interactions

No information.

Spacing

Territoriality

Defends burrow and the area outside of burrow that a bird facing out of it can reach ([Shallenberger 1973](#)).

Individual Distance

No information.

Sexual Behavior

Mating System And Sex Ratio

Monogamous. Breeding begins at 4 yr of age ([Floyd and Swanson 1983](#)). No information on sex ratio.

Pair Bond

Courtship Displays and Mate-Guarding. In Hawaiian Is., digging plays a part in early courtship and maintenance of pair bond. Some individuals can distinguish between odor of mate and that of unfamiliar birds ([Shallenberger 1973](#)). During day, pair may sit near burrow entrance and "coo" constantly while rubbing each other's head and neck ([Harrison 1990](#)). White feathers around eye may attract partner to preen ([Shallenberger 1973](#)). At night, pairs sit on ground opposite each other, puffing up their throats and uttering prolonged 2-part wailing duets that rise and fall in volume (see Sounds: vocalizations, above).

Copulation; Pre- and Postcopulatory Displays. See also Breeding: phenology, below. On Mānana I., begins with nibbling of head and neck of female by male, followed by placement of male's head over female's neck. With bill pointed down, male rubs head-and-neck-feathers of female. Male mounts female and treads on her back; shifts bill movement to top of female's head. Swipes bill back and forth across female's outstretched bill. Male opens wings and slides backward, and the 2 birds match cloacas. Female holds her tail up and to side; male's tail is forced down. Copulation is followed by much self-and mutual preening ([Shallenberger 1973](#)).

Duration and Maintenance of Pair Bond. Mate fidelity is documented in 4 out of 5 birds ([Shallenberger 1973](#)). Breeding success influences mate fidelity; pairs that do not lay or that lose eggs have poor mate fidelity the following year. Successful incubation rather than successful rearing of nestling seems to be critical in preserving the pair bond ([Fry et al. 1986a](#)).

Extra-Pair Copulations

Promiscuous courting occurs on Christmas I. ([Gallagher 1960](#)).

Social And Interspecific Behavior

Degree Of Sociality

Individual birds can distinguish others by odor ([Shallenberger 1973](#)). Most (66.9%) sightings of birds at sea are of single specimens; most birds seen at sea are traveling, generally singly or in small groups ([King 1974](#)). Feeding flocks of birds are seen in Hawaiian waters, largest flock consisting of 3,500 birds near Ka'ula Rock (islet in main Hawaiian Is.). Most (71.4%) flocks of >100 birds are within 1 d of travel of Hawaiian Is.

Play

Pecking the ground and collecting nest material are behaviors seen in breeders and nonbreeders ([Shallenberger 1973](#)).

Nonpredatory Interspecific Interactions

Distribution on Mānana I. off O'ahu was more extensive before colonization by Sooty Terns in late 1940s. Sooty Tern activity flattens vegetation and leads to collapse of burrows in loose soil. In 1970 and 1971, Sooty Terns colonized an area that was densely occupied by shearwaters alone in 1969. Aggressive toward hares (*Oryctolagus cuniculus*; [Shallenberger 1973](#)). Wedge-tailed Shearwaters reclaim burrows occupied by Bonin Petrels (*Pterodroma hypoleuca*) at Midway Is. and other atolls in Northwestern Hawaiian Is.; on Laysan I., petrel nestlings injured, killed, or evicted by shearwaters ([Shallenberger 1984](#), M. Morin pers. comm.). On Eastern I., Midway, Wedge-tailed and Christmas shearwaters nest under naupaka (*Scaevola*) bushes ([Shallenberger 1973](#)). On Christmas I., nest sites usually intermingled with those of Christmas Shearwaters and Phoenix Petrel (*Pterodroma alba*), but sometimes separate ([Gallagher 1960](#)). One Wedge-tailed Shearwater seen to copulate with Christmas Shearwater on Christmas I. ([Gallagher 1960](#)).

Predation

Kinds Of Predators

Rats (*Rattus rattus*) were introduced to Midway Is. in 1943 ([Fisher and Baldwin 1946](#)), and subsequently devastated Wedge-tailed Shearwater colonies there ([Haley 1984](#), [Harrison 1990](#)). Rat holes reported in empty burrows on Christmas I. ([Gallagher 1960](#)).

Domestic dogs (*Canis familiaris*) and cats (*Felis catus*) have been significant predators at Kauea Pt., Kaua'i I., HI, and continue to be so elsewhere on Kaua'i when control measures are lacking ([Byrd and Boynton 1979](#)). Erosion of soil caused by livestock is also a factor. Great Frigatebirds (*Fregata minor*) chase Wedge-tailed Shearwater individuals returning to colony before dark; none killed, but some forced to give up food. Black-crowned Night-Heron (*Nycticorax nycticorax*) may be predator on Mānana I. off O'ahu I. ([Whittow 1992](#)). Heavy predation by feral cats on Christmas I.; cats actually live in shearwater burrows ([Perry 1980](#), [Garnett 1984](#)).

Manner Of Predation

Dogs, cats, and rats, prey on adults. Frigatebirds prey on nestlings on Moku Manu I. in main Hawaiian Is., and in Northwestern Hawaiian Is. ([Shallenberger 1973](#)). On Kaua'i I., Common Mynas (*Acridotheres tristis*) prey on eggs, and Barn Owls (*Tyto alba*) on nestlings ([Byrd 1979](#), [Byrd and Boynton 1979](#), [Byrd and Telfer 1980](#)).

Response To Predators

No information.

Breeding

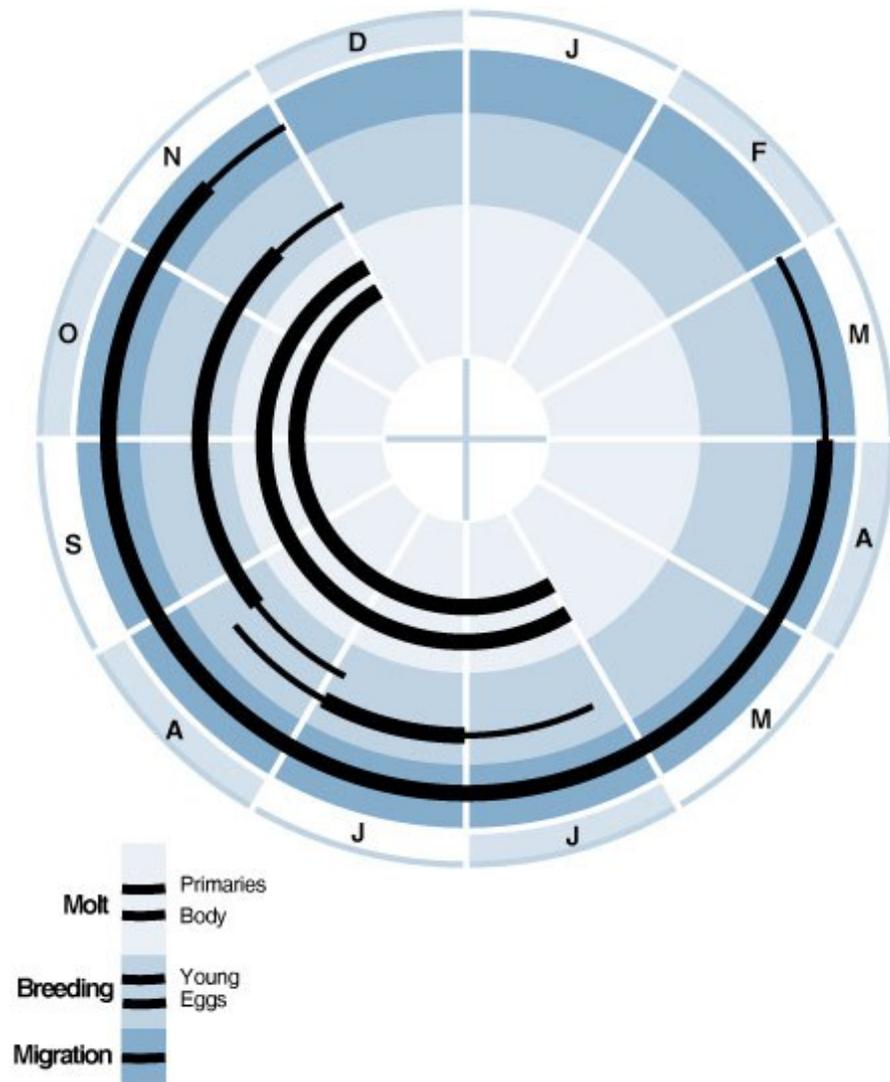


Figure 5. Annual cycle of breeding, migration, and molt of Wedge-tailed Shearwater in Hawaiian Is.

Phenology

Breeds Feb–Nov in Northern Hemisphere ([Fig. 5](#)); Aug–Oct to May–Jun in Southern Hemisphere. Breeding cycles are less strictly seasonal in equatorial birds than in birds at higher latitudes ([Murphy 1951](#)).

Pair Formation; Nest-Building

On Kaua‘i I., earliest sighting (1977–1981) varied from 28 Feb to 12 Mar ([Byrd et al. 1983](#)). Numbers build up gradually on Mānana I. near Honolulu, and on O‘ahu I. At night, rarely in burrows during first week. Adult breeding birds are among the first to arrive. Two members of a pair arrive separately. Both sexes are present intermittently during prelaying period. Tend to visit more exposed burrows first. As little as 1 wk after arrival, individual birds and occasionally pairs remain in burrows during day. By early Apr, have begun collecting nesting materials, and

evening flights over colony involve many birds. Courtship behavior is common. By mid-Apr, burrow occupancy during day is 80% pairs.

Daytime surface activity increases during this period, although most birds move in and out with evening and morning flights, respectively. During Apr and May, breeding burrow is often left unoccupied. In late Apr and May on Mānana I., nighttime activity increases; many prebreeding birds arrive ([Shallenberger 1973](#)). Aggressive encounters with intruders are more frequent and more prolonged in May when nonbreeders are more common. Pairs copulate in May (beginning mid-Apr), especially in early morning and late evening; copulation peaks in last week in May ([Shallenberger 1973](#)). Breeding schedule on Revillagigedo Is. (San Benedicto I.) is similar to that in Hawaiian Is. ([King 1974](#)). On Christmas I., begins visiting burrows at night in Dec. In Feb, most burrows are occupied by 1 bird during day. By Mar, pairs are common in burrows during day. In Apr, all burrows are occupied ([Gallagher 1960, Schreiber and Ashmole 1970](#)). In May, birds are common on ground during day.

First/Only Brood Per Season

First eggs at K&299lauea Pt., Kaua‘i I., HI, were laid 6–10 Jun during period 1977–1981 ([Fig. 5](#)). Peak egg-laying period: 12–18 Jun; most egg-laying completed by 25 Jun; peak egg-laying may be slightly later at western end of Hawaiian Archipelago ([Byrd et al. 1983](#)). On Mānana I. off O‘ahu, first egg laid 11 Jun, and 86% of eggs laid within 2 wk ([Shallenberger 1973](#)). On Christmas I., first egg laid in Apr ([Gallagher 1960, Schreiber and Ashmole 1970](#)) but most eggs laid in May. Farther south, in Phoenix Is., eggs laid in late Nov ([King 1974](#)).

Hatching. Eggs begin to hatch in late Jul; hatching peaks between 1 and 12 Aug, and most eggs hatch by 18 Aug at Klauea Pt.

Departure of Young from Nest or Cessation of Close Parental Care. At Klauea Pt. on Kaua‘i I., fledging begins in early Nov ([Fig. 5](#)), peaking between 13 and 27 Nov ([Byrd et al. 1983](#)). On Christmas I., fledging is complete by end of Nov ([Gallagher 1960, Schreiber and Ashmole 1970](#)).

By early Nov in central Pacific, no adults visit breeding island; fledglings have gone by mid-Nov ([King 1974](#)).

Second/Later Broods Per Season

None.

Nest Site

Selection Process

In Hawaiian Is., most birds return to natal island to breed ([Munro 1967](#)). Of 38 banded birds recovered on Mānana I. off O‘ahu, all had been banded there ([Shallenberger 1973](#)). Readily nests in artificial burrows at Klauea Pt. on Kaua‘i I. with higher-than-average nesting success ([Byrd 1979](#)). Some birds can find their burrows when released within sight of their nesting colony, after their olfactory nerves have been cut ([Shallenberger 1975](#)), suggesting that vision is

important in burrow recognition while sense of smell is not. However, some birds can detect odor of their own nest materials ([Shallenberger 1975](#)).

Microhabitat

Although most birds nest in burrows in ground (see below), some do nest on surface, particularly in crowded colonies where nest sites are scarce, where ground is difficult to excavate, or when burrow has been blocked by storm-driven sand and rocks ([Oliver 1955](#)). Surface nests are often in partial or complete shade of grass tussocks on Mānana I., 'ilima (*Sida fallax*) bushes on Canton I. in Phoenix Is., and naupaka bushes on Midway Is. ([Shallenberger 1973](#)). Only those surface nests that are shaded are likely to be successful ([Shallenberger 1973](#)).

Site Characteristics

Nest sites are usually at sea level. Most nests in burrows are in sand or soil, but there is much variation in choice of nest site. On Mānana I. off O'ahu, uses natural rock crevices, sand burrows, shallow burrows in volcanic soil (see [Fig. 6](#)) covered with tall vegetation, surface nests in partial shade, and deep communal burrows in walls of rain gullies. Three burrow tunnels may exist one on top of the other ([Shallenberger 1973](#)). At Klauea Pt. on Kaua'i I., mean depth of nest is 50.0 cm ± 10.8 SD (range 31.0–78.0, $n = 19$; [Byrd et al. 1984](#)). Uses ledges and rock piles extensively on rocky islands such as Necker in Northwestern Hawaiian Is. ([Harrison 1990](#)), where there are few areas amenable to excavation of burrows. On Christmas I., uses burrows in shell debris or crevices under natural coral ledges ([Gallagher 1960](#)).

Nest

Construction Process

Both adults share in excavation of burrow, using bills and feet ([Shallenberger 1984](#)). Uses beak to loosen soil and feet to scrape and remove soil. Inserts bill into soil and shakes it. While digging, leans to one side with tail-feathers high in air. Swings upper leg back and forth at rate of 1.5–2 kicks/s. Uses 1 leg 5–20 s before shifting to other leg. Digs for up to 16 min; usually stops after 3–4 min. Burrow excavation concentrated during first month of return to breeding colony. Members of pair may alternate digging activities. Both members accumulate dirt and callus along side of tarsus and bottom of feet ([Shallenberger 1973](#)). Tarsi are long and strong, and are well adapted to digging. Does not use beak as much as feet for digging ([Gross et al. 1963](#)).

Structure And Composition Matter

In Hawaiian Is., first part of burrow usually slopes gently down toward nesting chamber ([Harrison 1990](#)). Not all nesting chambers are lined. Nest material collected mainly in evening, both members of pair participating. Collection continues intermittently during incubation. Collects vegetation in vicinity of burrow. On Mānana I. off O'ahu, collects sourgrass (*Digitaria insularis*) stems and leaves, and sandbur (*Cenchrus echinatus*). Does not seem to carry plant material in flight ([Shallenberger 1973](#)). On Christmas I., not all nest chambers are lined with grass or twigs ([Gallagher 1960](#)).

Dimensions

Burrow dimensions at Klauea Pt. on Kaua‘i I.: width of entrance, 19.4 cm \pm 3.2 SD (range 11.0–26.0, $n = 64$); height of entrance, 12.0 cm \pm 2.3 SD (range 8.0–15.0, $n = 64$; [Byrd et al. 1984](#)). On Mānana I. off O‘ahu, burrow length may be as long as 5.18 m, but most burrows in the crater are slightly <1 m long. On crater slopes (see [Fig. 3](#)) mean length of burrow is 45.7 cm, width of opening 20.3–30.5 cm, and entrance height 10.2–22.9 cm ([Shallenberger 1973](#)). Diameter of nesting chamber on Mānana I. is 27.9–45.7 cm ([Shallenberger 1973](#)).

Burrow Density

On Mānana I., 0.28 burrow/m² ([Shallenberger 1973](#)).

Microclimate

Mean air temperature in occupied burrows on Mānana I. is 29.1°C \pm 1.23 SD during day, cooling to 26°C at night ($n = 16$; [Whittow et al. 1982](#)). Partial pressures of oxygen and carbon dioxide in burrow air are 149.3 and 0.5 torr, respectively ([Whittow 1984b](#)).

Maintenance Or Reuse Of Nests, Alternate Nests

Heavy rainfall, high winds, people, terns, and other shearwaters take heavy toll on shearwater burrows during winter on Mānana I. and at Klauea Pt., Kaua‘i I. Reexcavation results in many connected burrows with multiple entrances ([Shallenberger 1973](#), [Whittow 1979](#), [Byrd et al. 1983](#)). On Mānana I., 14 out of 32 banded birds recovered the following year were in the same burrow; 11 were in burrows ≤ 3.1 m away; 6 birds were on surface close to original burrow ([Shallenberger 1973](#)). In another study, average distance between burrows for birds that changed burrows from one year to next was 8.2 m ([Fry et al. 1986b](#)).

Nonbreeding Nests

Nonbreeding birds lengthen old burrows or dig new ones as late as mid-Sep on Mānana I. ([Shallenberger 1973](#)). On Christmas I., 65% of burrows are unoccupied ([Schreiber and Ashmole 1970](#)).

Eggs

Shape

Long, oval.

Size

At Klauea Pt. on Kaua‘i I., mean egg length is 61.4 mm \pm 1.7 SD ($n = 79$), and width 41.1 mm \pm 1.2 SD ($n = 79$; [Byrd et al. 1984](#)).

Mass

Mean weight of freshly laid egg is 60.04 g \pm 3.32 SD ($n = 27$), and mean volume is 54.25 ml \pm 14.17 SD ($n = 65$; [Ackerman et al. 1980](#)). Egg represents 15.4% of adult mass. Egg contents account for 92.7% of egg mass, and yolk makes up 40.0% of content. Water makes up 73.2% of composition of egg contents; energy content of egg is 427.3 kJ ([Pettit et al. 1984c](#)).



Color

White (see [Fig. 6](#)); often becomes stained by soil in burrow or by bird's feathers and incubation patch ([Berger 1981](#)).

Surface Texture

Matte surface.

Eggshell Thickness

Shells are thin (0.21 mm)—64.6% of the thickness expected for an egg the size of the shearwater's ([Whittow et al. 1982](#)). Shell mass (3.71 g) also low: 74.7% of the predicted value for a 60-g egg ([Whittow et al. 1982](#)).

Figure 6. *Wedge-Tailed Shearwater egg; Laysan Is., Hawaii.*

Egg Temperature

Mean egg temperature is $35.0^{\circ}\text{C} \pm 1.5$ SD ($n = 59$; [Whittow et al. 1982](#)), close to average value for Procellariiformes.

Clutch Size

One.

Egg-Laying

Prelying Exodus. Activity in colony on Mānana I. off O'ahu drops dramatically in late May, when active breeders leave on prelying exodus ([Shallenberger 1984](#)); burrow occupancy 2–11 Jun is only 0.5–3.0%. Flights into colony in evening are reduced and nocturnal calls low; most birds in colony are not attached to burrows—probably immature or nonbreeding. Little daytime activity. Both males and females are away. On Mānana I. off O'ahu, male usually arrives back from prelying exodus first ([Shallenberger 1973](#)). Yolk formation takes 21–23 d, and prelying exodus from colony lasts 28 d in North Pacific ([Fry et al. 1986b](#)).

Time of Day. No information for North Pacific; most eggs laid at night in Kermadec Is. (South Pacific; [Crockett 1975](#)).

Replacement of Individual Eggs. Only 1 instance of re-laying by a banded female bird recorded on Mānana I.; new egg laid 8 d after original egg was removed, but burrow was later abandoned ([Shallenberger 1973](#)).

Incubation

Onset Of Broodiness And Incubation In Relation To Laying

Gonadal development in Hawaiian birds begins when birds return to breeding island and peaks in May, a month before eggs are laid. After May, gonads decrease in size, but decrease is arrested

from Jul to Oct. Thereafter, gonads shrink rapidly ([King 1974](#)). Incubation begins immediately after the single egg is laid.

Incubation Patches

Both adults have incubation patch ([Berger 1981](#)). Mean temperature of incubation patch during day at Midway Is. is 37.8°C, 3.5°C higher than egg temperature and 1.7°C lower than adult body temperature ([Howell and Bartholomew 1961](#)). Mean temperature of incubation patch on Mānana I. off O‘ahu is 37.6°C ([Whittow et al. 1982](#)).

Incubation Period

Incubation period on Mānana I. is 52.4 d (range 48–56, $n = 17$; [Shallenberger 1973](#)). Average incubation period at Klauea Pt. on Kaua‘i I. is 53 d (range 51–55, $n = 6$; [Byrd et al. 1983](#)). Incubation is prolonged, congruent with scarce, distant food supply; incubation period is 179% of expected value for an egg weighing 60 g, on basis of data from 161 species of birds ([Whittow 1980](#)). Many features of egg are related to its long incubation period.

Egg Mass Loss During Incubation

Eggs lose mass at rate of 154.6 mg/d during incubation. This rate is lower than expected for a 60-g egg, and low even by procellariiform standards ([Whittow et al. 1982](#), [Rahn and Whittow 1988](#)). Low mass loss is due to low water vapor conductance of shell (6.12 mg/d torr), which results from a low total functional pore area (0.71 m², 37.9% of expected value, and fewer pores in shell [3,587 pores/egg]; [Whittow et al. 1982](#), [Whittow 1984b](#)). Decrease in egg mass is due to loss of water vapor from egg through microscopic pores in shell. Water vapor pressure in immediate vicinity of incubated egg is 19.6 torr ([Whittow et al. 1982](#)). Nest ventilation required to keep water vapor pressure down to this level is 70.9 l/d ([Whittow 1984b](#)), achieved by small postural movements of incubating bird. Embryo produces 5.5 g water during incubation by oxidation of lipids in egg. Total mass loss of egg during incubation is 10.7 g—17.2% of mass of freshly laid egg ([Pettit and Whittow 1983](#), [Whittow 1984b](#)).

Embryonic Growth And Metabolism

Embryonic growth is most rapid (1.4 g/d) on thirty-sixth day of incubation ([Ackerman et al. 1980](#)). Embryonic organ growth is greatest in stomach and least in heart and lungs ([Zhang and Whittow 1992](#)). Oxygen consumption of egg increases as embryo grows. Total oxygen consumption of egg during incubation is 132% of expected value, reflecting prolonged incubation and cost of maintenance of an embryo over long period ([Pettit et al. 1982](#)).

Parental Behavior

In Hawaiian Is., first incubation shift is taken by male more often than by female ([Shallenberger 1973](#)). Incubation shifts may last as long as 13 d ([Shallenberger 1973](#)). Mate often sits near incubating bird ([Berger 1981](#)). Attempts at incubating 2 eggs are always unsuccessful for both eggs ([Shallenberger 1973](#)). Readily incubates eggs of other conspecifics; does not distinguish between its own and other eggs ([Shallenberger 1973](#)). Also incubates eggs of Newell’s Shearwaters that are substituted for its own eggs; these eggs hatch successfully and are reared to fledging ([Byrd et al. 1984](#)).

Before and during incubation, birds leave burrows, pick at vegetation, and sometimes toss plants to their side or over their backs. Latter behavior is seen in both breeders and nonbreeders. Incubating birds often leave egg and burrow in evening, defecate, preen themselves, and return to egg. This behavior is often accompanied by ground-pecking and litter-tossing ([Shallenberger 1973](#)). Breeding birds dig intermittently while incubating; on returning to burrow, may dig for 20–30 s to remove soil in entrance to burrow ([Shallenberger 1973](#)). At night, most birds (76.3%) face out toward entrance of burrow; during day, proportion drops to 36% ([Shallenberger 1973](#)). Birds themselves may accidentally damage egg ([Shallenberger 1973](#)). Incubating bird loses 0.33% of body mass during incubation ([Ellis et al. 1983](#)).

Hardiness Of Eggs Against Temperature Stress; Effect Of Egg Neglect

Egg has no ability to increase its oxygen consumption and metabolic heat production in response to cooling until it has hatched or is in the process of hatching. Embryonic body temperature diminishes with environmental temperature in an ectothermic manner ([Mathiu et al. 1992](#)). Eggs may be temporarily abandoned, particularly during daylight. Abandonment is most common among shallow nesters on hot days ([Shallenberger 1973](#)). One egg on Mānana I. off O‘ahu had been observed to be neglected and was cool to the touch; it pipped on day 53 after laying and took 61 d to hatch ([Ackerman et al. 1980](#)). If egg is removed, adults may be seen in burrow as many as 21 d after its removal. Substitution of plastic egg results in prolonged incubation. An egg added to burrow containing a hatchling is incubated ([Shallenberger 1973](#)). If mate does not return, care of egg is prolonged, but embryo always dies ([Shallenberger 1973](#)).

Hatching

Preliminary Events And Vocalizations

Parental calls are most frequent immediately before and after hatching ([Shallenberger 1973](#)).

Shell-Breaking And Emergence

On average, initial event during pipping of egg is star fracture of shell on day 47 of incubation. This “external pipping” is extended, and on day 48 embryo’s beak pierces internal shell membrane (internal pipping), permitting embryo to begin using its lungs to breathe air in air cell. On day 50, pip hole forms in eggshell so that embryo can breathe fresh air, and on day 52 egg hatches. Entire pipping process takes $5.6 \text{ d} \pm 1.2 \text{ SD}$ ($n = 27$; [Pettit and Whittow 1983](#)).

Pipping is a critical period in life history of egg; profound changes occur, and some embryos die in pipped eggs ([Shallenberger 1973](#)). Although pipping accounts for 10.6% of total incubation period, 29.0% of total decrease in egg mass occurs after egg has pipped ([Pettit et al. 1982](#), [Pettit and Whittow 1983](#), [Whittow et al. 1982](#)).

After pipping, oxygen consumption of egg increases a great amount, and embryonic intestine grows rapidly ([Zhang and Whittow 1992](#)). A large part (42.4%) of total oxygen consumption of egg during incubation occurs in pipped egg ([Ackerman et al. 1980](#), [Whittow 1984b](#)).

Respiratory tidal and minute volumes, but not respiratory frequency, increase in eggs with pip holes compared with those that have recently pipped internally; increase further when egg hatches ([Pettit and Whittow 1982b](#)). Partial pressures of oxygen and carbon dioxide in air cell

immediately before pipping are 101 and 42 torr, respectively ([Ackerman et al. 1980](#), [Paganelli and Rahn 1984](#)). Pipping has dramatic effect on composition of air in air cell of egg; star fracture of shell brings increase in oxygen and decrease in carbon dioxide pressures. Internal pipping reverses this trend, but when pip hole forms, gas in air cell approaches fresh air in composition ([Pettit and Whittow 1982a](#)).

Embryonic heart rate is approximately 210 beats/min before pipping; does not change as result of external pipping, but increases during internal pipping and when pip hole forms. Increases in heart rate are associated with increase in oxygen pulse (oxygen consumed at each heart beat; [Tazawa and Whittow 1994](#)).

Parental Assistance And Disposal Of Eggshells

Eggshell rarely removed, but some adults remove pieces of shells; pieces are inadvertently removed when bird digs ([Shallenberger 1973](#)).

Young Birds

Condition At Hatching

Mass. Mean hatchling mass on Mānana I. off O‘ahu is 39 g (range 34–43; [Shallenberger 1973](#)); or 39.1 g ± 3.9 SD ($n = 12$; [Ackerman et al. 1980](#)). Yolk reserve of hatchling is 8.75 g ± 0.57 SD ($n = 9$; [Ackerman et al. 1980](#)); estimated to be able to sustain hatchling for 5.7 d ([Pettit et al. 1984c](#)). Hatchling tissue is 75.3% water and contains 176.6 kJ of energy ([Pettit et al. 1984c](#)). Musculature of legs weighs almost 3 times as much as pectoral muscles ([Mathiu et al. 1992](#), [Zhang and Whittow 1992](#)).

Amount and Distribution of Feathers. Covered with light or dark gray down (protoptiles) that is lighter on underparts ([Kuroda 1954](#), [Pettit et al. 1984a](#)). Down represents 3% of hatchling’s body mass; it is longest on back and shortest on crown ([Mathiu et al. 1992](#)).

Color of Bare parts, Gape Markings, Condition of Eyes, Retention of Egg Tooth. Feet and tarsi flesh-colored; bill light slaty or bluish gray ([Shallenberger 1973](#), [Pettit et al. 1984a](#)). Eyes closed at hatching, but open 12–24 h later ([Shallenberger 1973](#), [Pettit et al. 1984a](#)). Egg tooth present (see below).

Degree of Coordinated Movement or Ability to Find Food. Chick can support itself within 24 h of hatching.

Responses, Body Attitude. Hatchlings respond to increased carbon dioxide in air they breathe by increasing their pulmonary ventilation ([Pettit and Whittow 1982b](#)).

Body Temperature and Metabolism. Body temperature (35.1–37.3°C) is within zone of thermal neutrality (29–36°C); lower than temperature of adults (39.1°C; [Mathiu et al. 1992](#)). Metabolic rate of hatchlings (16.9 kJ/d) is also lower than that of adult, after correction for difference in body size ([Mathiu et al. 1992](#)). Thermoregulatory ability improves dramatically on hatching: hatchlings increase metabolic heat production in response to cooling (cold-induced thermogenesis) by as much as 75%. Hatchlings also respond to heat exposure by panting ([Mathiu](#)

[et al. 1992](#)). Hatchlings are surpassed by adults in thermogenic capacity; also in effectiveness of evaporative cooling, associated with lower panting frequencies in hatchling ([Mathiu et al. 1992](#)).

Growth And Development

After first day, nestling can move about. Body mass increases to maximal value of $565.7 \text{ g} \pm 43.0 \text{ SD}$ ($n = 37$) at Klauea Pt. on Kaua‘i I., at nestling age of 86.8 d. Mass then declines to $428.8 \text{ g} \pm 54.1 \text{ SD}$ ($n = 33$) at fledging (age 109.2 d). Maximal mass and fledging mass were lower on Mānana I. off O‘ahu and higher at French Frigate Shoals than at Klauea Pt. ([Pettit et al. 1984a](#)). No decline in body mass before fledging on Mānana I., according to Shallenberger ([1973](#)). A captive, hand-reared nestling in Hawaii that was allowed to eat as much as it wanted, voluntarily reduced food intake after day 90; reduced food intake was accompanied by decline in body mass (J. L. Sincock, R. Sincock, and G. V. Byrd pers. comm.). Extremely underweight nestlings found in Sep and Oct on Mānana I., probably because of lack of food ([Shallenberger 1973](#)). Growth of toe, culmen, tibia-fibula, and tarsometatarsus levels off by the time that body mass peaks, but wing and tail continue to grow. Egg tooth disappears at mean age of $34.9 \text{ d} \pm 3.7 \text{ SD}$ ($n = 15$; [Pettit et al. 1984a](#)).

Late nestlings that are forced to leave their burrows after heavy rain indulge in heavy wing-flapping, presumably to aid in drying but possibly to increase metabolic heat production. In these circumstances, many nestlings may have no protection from either further rain or solar radiation ([Whittow 1979](#)).

Older nestlings often peck the ground and collect nest material, functional precursors of nest building ([Shallenberger 1973](#)). Nestlings close to fledging excavate burrows; possibly assisted by parents. Nestlings call frequently throughout nestling period, begging from passing adults. Nestlings defend burrow with vocalizations and pecking ([Shallenberger 1973](#)).

Parental Care

Brooding

One or both parents remain with nestling as long as 6 d after hatching, although after third day attendance is intermittent. The following week, a parent visits every night ([Shallenberger 1973](#)).

Feeding

Nestlings are initially fed stomach oil by regurgitation from adult ([Pettit et al. 1984a](#)). For first 3–4 d, adult initiates feeding by picking up nestling’s bill. Subsequently, nestling vocalizes and pecks at adult’s bill and throat. Nestling inserts bill crosswise into parent’s bill. Nestling is fed 8–10 times at 15-to 20-s intervals. Mean feeding interval at Tern I., French Frigate Shoals, is $1.7 \text{ d} \pm 0.4 \text{ SD}$ (range 1–11, $n = 10$ nestlings); at Klauea Pt. on Kaua‘i I., 1.3 d ([Pettit et al. 1984a](#)). Mean gain in body mass per feeding is $40.0 \text{ g} \pm 11.4 \text{ SD}$ ($n = 56$ feedings; [Pettit et al. 1984a](#)).

Older nestlings may be fed outside burrow entrance. Adult preens chick before feeding it ([Shallenberger 1973](#)). On Mānana I. off O‘ahu, nestlings are fed with decreasing frequency as they get older ([Shallenberger 1984](#)).

Nest Sanitation

Burrow remains clean during incubation period. Birds defecate outside of burrow entrance. Incubating birds leave egg, turn at entrance of burrow, and defecate while leaning with head toward burrow entrance. Usually defecate early in evening ([Shallenberger 1973](#)). Young nestlings defecate on walls of nest chamber, tipping forward before doing so, so that excreta are expelled on upper part of burrow wall, leaving nest chamber clean; older nestlings defecate at burrow entrance ([Shallenberger 1973](#)).

Carrying Of Young

Does not occur.

Cooperative Breeding

Does not occur.

Brood Parasitism

Does not occur.

Fledgling Stage

Departure From Nest

Age at Departure. At Klauea Pt. on Kaua‘i I., nestling period ranges from 103 to 115 d, averaging 109.2, 107.1, and 106.2 d in 3 different years (1978, 1979, 1980) ([Byrd et al. 1983](#)). At Kure I., range is 99–111 d ($n = 10$; [Woodward 1972](#)).

Condition of Development at Departure. Fledglings are indistinguishable from adults, except for traces of down ([Munro 1967](#)). In Hawaiian Is., some late fledglings are underweight, suggesting that adults have stopped attending colonies and may have left the area ([Shallenberger 1973](#)).

Growth

Mean fledgling mass is $420.1 \text{ g} \pm 43.6 \text{ SD}$ (range 280–500, $n = 65$; [Byrd et al. 1984](#)). Varies from year to year and at different sites in Hawaiian Is. ([Pettit et al. 1984a](#)).

Association With Parents Or Other Young

See above.

Ability To Get Around, Feed, And Care For Self

Fledglings from Mānana I. are attracted to lights on O‘ahu I. ([Shallenberger 1973](#)). Occasionally follow ships for ≥ 30 min near Hawaiian Is. ([King 1974](#)).

Immature Stage

No information.

Demography and Populations

Measures Of Breeding Activity

Age At First Breeding; Intervals Between Breeding

Breeding begins at 4 yr of age ([Floyd and Swanson 1983](#)).

Clutch

One egg per clutch; 1 clutch per season.

Annual And Lifetime Reproductive Success

Hatching success (eggs hatched/eggs laid) varied from 58.1 to 85.5% over 4-yr period in natural burrows at Klauea Pt. on Kaua'i I., and from 69.0 to 100% in artificial burrows ([Byrd et al. 1983](#)). Among surface-nesting birds at Tern I., French Frigate Shoals, in Northwestern Hawaiian Is., hatching success is 45% for shaded nests, 1.6–11.4% for poorly shaded sites ([Sievert 1996](#)). At Klauea Pt., < 81.0% of eggs that hatch result in fledglings ([Byrd et al. 1983](#)); as many as 79.6% of eggs laid in natural burrows result in fledglings, but in some years this figure can be as low as 46.8% ([Byrd et al. 1983](#)). In artificial burrows, ratio of fledglings to eggs laid may be as high as 93.3%. Most loss of fledgling production is due to egg loss. At Kure I., ratio for natural burrows is 80% ([Byrd et al. 1983](#)).

Number Of Broods Normally Reared Per Season

One.

Proportion Of Total Females That Rear At Least One Brood To Nest-Leaving Or Independence

No information.

Life Span And Survivorship

Oldest banded bird recovered was 29 yr old (from Laysan I., 1994; E. N. Flint pers. comm.). Longevity may be greater than indicated by banding studies, since bands are lost or opened when birds dig burrows ([Fry and Swenson 1989](#)).

Disease And Body Parasites

Diseases

No evidence of disease on Mānana I. off O'ahu ([Shallenberger 1973](#)).

Body Parasites

Ectoparasites associated with Wedge-tailed Shearwaters in Hawaiian Is. include: Acari—*Ornithodoros capensis*, *Hypozetes laysanensis*, *Scapheraemus sinusus*, *Galumna flabellifera*, *Multioplia wilsoni*, *Nesorbatula pacifica* ([Goff 1987](#)); Mallophaga—*Halipeurus mirabilis*, *Longimenopon puffinus*, *Trabeculus mirabilis*; Hippoboscidae—*Olfersia aenescens* ([van Riper and van Riper 1985](#)).

Causes Of Mortality

Exposure

Some nestlings wander from burrow or roll down slope in ground and are unable to find their way back; may die from starvation or hyperthermia, since solar radiation is intense ([Shallenberger 1973](#), [Byrd et al.](#)

1983, [Whittow et al. 1992](#)). Nestlings can be buried by mud after heavy rain ([Whittow 1979](#), [Whittow et al. 1992](#)), when as many as half of all burrows may collapse. At Klauea Pt. on Kaua'i I. ([Byrd et al. 1983](#)), destruction of burrows as result of human intrusion or heavy rainfall is major cause of nestling mortality. Older nestlings may be obliged to leave breeding colony prematurely and perish at sea after forced evacuation of their burrows by heavy rain ([Hadley 1961](#)). Younger nestlings may be particularly susceptible to rain damage because their plumage (down) is less waterproof.

Predation

Sharks are serious threat to fledglings in Northwestern Hawaiian Is. ([Shallenberger 1973](#)). Barn Owls prey on nestlings at Klauea Pt. ([Byrd and Telfer 1980](#)); dogs destroy both nestlings and adults ([Byrd and Boynton 1979](#)).

Competition With Other Species

No evidence.

Other Causes

In Hawaiian Is., collisions with other birds may paralyze or kill. Shearwaters are killed, injured, or disoriented when they collide with lighted buildings, lighthouses, boats, or field lights, or when fledglings gather on lighted roads in Nov and Dec. Some birds are crushed by cars. Birds show a photonegative response to a low-power flashlight but freeze in response to a high-power flashlight or, presumably, to streetlights ([Shallenberger 1973](#)). Attached double embryos (Siamese twins) can occur ([Pettit and Whittow 1981](#)), but none survive.

Range

Initial Dispersal From Natal Site

Fledglings fly out to sea or walk down to ocean. Fledglings in Kermadec Is. leave burrows and walk to edge of cliff; many fall into sea ([Oliver 1955](#)).

Fidelity To Breeding Site And Winter Home Range

Return to same colonies year after year, often to same burrow ([Shallenberger 1984](#)). See Breeding: nest site, and Breeding: nest, above. Most birds migrate at end of breeding season, but a few may remain (see Migration, above). Birds banded at both Klauea Pt. on Kaua'i I. and French Frigate Shoals are recaptured at Kure I., a distance of 1,995 km and 705 km, respectively ([Amerson 1971](#), [Woodward 1972](#)). There is also movement between Johnston Atoll and French Frigate Shoals, a distance of 738 km ([Amerson and Shelton 1976](#)).

Home Range

During breeding season, home range must include burrow and entrance, but no definitive information.

Population Status

Numbers

Counting birds at sea is difficult; even establishing occupancy of long burrows in a breeding colony often requires use of special video equipment ([Dyer and Hill 1991](#)). Paucity of information for Indian Ocean, and total Australian and South Pacific populations, militate against assessment of worldwide total population. Population in Hawaiian Archipelago is best known: total from Harrison's ([1990](#)) figures is 1,330,340 (maximum). Wedge-tailed Shearwater accounts for 17% of total Hawaiian seabird population ([Harrison and](#)

[Seki 1987](#)). Nonbreeders account for more than half the population ([King 1974](#)). Published figures: for Pacific Ocean, excluding Hawaii, 2.29 million birds; for Australia, 1.43 million; for Indian Ocean (Cousin I., Round I., Boudeuse I.), 146,000. Combined figures give estimate of 5.2 million for worldwide population—probably a large underestimate.

Trends

Population on Midway Is. increased from 5,000 in 1922 to 62,000 in 1945 despite destruction of habitat during World War II. Today, population only about 3,000, probably because of predation by black rats (*Rattus rattus*; [Fisher and Baldwin 1946](#), [Harrison 1990](#)). On Laysan I. and Lisianski I., also in Northwestern Hawaiian Is., population declined in 1920s and 1930s, as result of loss of vegetation ([Harrison et al. 1984](#)). Population increased on Mānana I. off O‘ahu from zero in 1900 to >20,000 pairs in 1984, after consumption of birds for food ceased ([Harrison et al. 1984](#)). Hawaiian populations probably stable at present ([Harrison 1990](#)). Population is seasonal: In Hawaiian Is., number of birds reaches maximum in May; on Johnston Atoll, in Aug ([King 1974](#)).

Population Regulation

Few data; needs study. On Christmas I., almost no birds fledged in El Niño year of 1982, when fish populations plummeted and birds were unable to feed their young ([King 1984](#)).

Conservation and Management

Effects Of Human Activity

Shooting And Trapping

Early Hawaiians relished young birds ([Shallenberger 1984](#)). Feather hunters accounted for destruction of large numbers of birds at Midway Is. at beginning of twentieth century ([Fisher 1949](#)). During World War II, eggs were collected and eaten on Midway Is. ([Fisher and Baldwin 1946](#)).

Pesticides And Other Contaminants/Toxics

Breast-feathers of birds on Mānana I. off O‘ahu contain lead (mean 1,599 ppb [parts per billion] ± 356 SD), cadmium (292 ppb ± 52), selenium (3,227 ppb ± 139) and mercury (3,851 ppb ± 354; [Burger et al. 1992](#)). Mercury and cadmium levels are higher in shearwaters than in Brown Noddies and Sooty Terns on same breeding island. Lead levels are higher and mercury levels lower on Johnston Atoll ([Burger et al. 1992](#)).

Mercury levels in eggs laid in main Hawaiian Is. are higher than in Northwestern Hawaiian Is. Eggs also contain selenium (1.09–1.38 ppm), endrin, DDE and other PCBs. Higher concentration of DDE and broader array of organochlorides in shearwater eggs than in eggs of Sooty Terns and Red-footed Boobies ([Ohlendorf and Harrison 1982](#), [Harrison 1990](#)). Not known if there are any biological effects of these levels of pesticides.

Experimental application of weathered Santa Barbara crude oil to Wedge-tailed Shearwater plumage has no effect on length of its prelaying exodus, but only 16% of these birds laid eggs, and either the eggs did not hatch or hatching success was significantly lower ([Fry et al. 1983](#)); number of nestlings raised was also significantly lower. External application of oil significantly reduces number of birds returning to breed the following year, as well as number of birds incubating eggs. Effect of externally applied oil on percentage of birds that hatch eggs is related to amount of oil applied to plumage. Number of birds returning after prelaying exodus and

number of birds incubating eggs are significantly reduced after oral dose of 2 ml crude oil. However, growth rates of nestlings of birds given oral doses of oil were similar to those of untreated controls ([Fry et al. 1986b](#)).

Ingestion Of Plastics, Lead and Other Pollutants

Plastic objects 2–4 mm in diameter are found in gizzards or proventriculi of 60% of shearwaters on Mānana I. off O‘ahu. Most plastics are rounded pellets of polyethylene or polypropylene, but 20% are worn polystyrene. Squid beaks 1–2 mm long are present in 70% of the birds; the more squid beaks, the fewer the plastic objects. No difference between sexes in amount of plastic in digestive tract. No apparent ill effects of plastics. No regurgitated indigestible materials are seen in breeding colony ([Fry et al. 1987](#)). At Midway Is., most ingested plastic items that are recovered from proventriculi are white; green and blue are the second and third most common colors ([Sileo et al. 1990](#)). Less plastic in stomach contents at Johnston Atoll than at Midway Is.; Kaua‘i I. birds also have less plastic than do birds at Midway Is.; more plastic in stomach contents at Tern I., French Frigate Shoals, than at Nihoa I. in Northwestern Hawaiian Is. ([Sileo et al. 1990](#)).

Collisions With Stationary/Moving Structures Or Objects

On their first flight from nesting site, fledglings are confused by lights and collide with power lines in main Hawaiian Is.; land on roads and beaches. Birds collided with aircraft at Midway Is. during World War II ([Fisher 1949](#)); burrows, eggs, and birds were damaged by vehicles ([Fisher 1949](#)). Vehicles driving through colonies on Christmas I. ([Perry 1980](#)) are threat to burrows and birds.

Fishing Nets

No information.

Degradation Of Habitat

Burrows deteriorate during winter (see Breeding: nest, above).

Disturbance At Nest And Roost Sites

Collapse of burrows on Mānana I. off O‘ahu caused by visitors has been documented; also damage caused by vandals (Shallenberger [1971](#), [1973](#)).

Direct Human/Research Impacts

These “moaning birds” were disliked and persecuted by servicemen on Midway Is. ([Fisher and Baldwin 1946](#)). Birds and burrows were destroyed during World War II construction on Midway; the paving of much of Eastern I. obliterated many actual and potential nesting sites ([Fisher 1949](#)). Not all of the changes wrought by humans on Midway Is. have been detrimental; addition of 8.16 x 10⁶ kg of topsoil to Sand I. has provided more suitable habitat for burrow-nesting birds than native sand provides. Burrows in sand collapse easily and can be covered by blowing sand ([Fisher 1949](#)). Flocks are also useful to fishermen as an aid to finding schools of tuna in the Pacific ([Au and Pitman 1988](#)).

Management

Conservation Status

Future of this species is related to (1) maintenance of predatory fish, squid, and bait fish stocks ([Harrison 1990](#)); probably dependent on tuna to increase availability of small prey at surface ([Furness and Ainley 1984](#)); (2) effectiveness of predator control, vegetation management, and prevention of burrow and habitat destruction

by people ([Warham 1990](#)). Whittow et al. ([1995](#)) believe that extensive growth of golden crown-beard (*Verbesina encelioides*) might interfere with flight and burrowing activities on Mānana I. off O‘ahu.

Measures Proposed And Taken

In Hawaii, when eggs of domestic fowl that have been treated with bird repellent are placed in shearwater colonies, predation of shearwater eggs by Common Mynas is reduced ([Byrd and Moriarty 1980](#)). Fledglings landing on roads and beaches on O‘ahu are brought to the oceanarium Sea Life Park, which functions as a rehabilitation center.

Effectiveness Of Measures

See above.

Appearance

Molts And Plumage

Hatchlings

At hatching, covered with light or dark gray down (protopiles) that is lighter on underparts ([Kuroda 1954](#), [Pettit et al. 1984a](#)). Secondary down (mesoptiles) dark gray; appears after 30–35 d ([Shallenberger 1973](#)); or, according to Pettit et al. ([1984a](#)), 22.6 d \pm 3.9 SD ($n = 22$).

Juvenal Plumage

Prejuvenal molt begins when pin-feathers of primary and secondary flight-feathers and rectrices begin to emerge at mean age of 34.9 d \pm 3.7 SD ($n = 15$), although nestlings are covered with down until 75–85 d old ([Pettit et al. 1984a](#)).

First-year birds probably retain Juvenal plumage for 15 mo ([King 1974](#)).

Definitive Basic Plumage

Molt takes place mainly outside of breeding season (and therefore at sea; thus it is difficult to document). Probably begins in Dec in North Pacific (in Dec, birds have fresh plumage, including remiges and rectrices with a silvery sheen and prominent white scalloping on lower back and scapulars); it is almost complete when birds return to central Pacific to breed ([King 1974](#)).

In e. Pacific, inner primaries molt in Feb; in central Pacific, growth of primaries completed in Mar (remiges in Apr). Primary molt more symmetrical than rectrix molt. In distal molt (P7–P10), one feather is replaced at a time. Inner primaries can be replaced simultaneously. Remiges have broad vanes and blunt tips with sharp central points indicative of unworn feathers ([King 1974](#)). No flight-feather molt between Jun and Dec. Rectrix replacement follows no fixed sequence. Replacement of rectrices continues in Apr.

Molt of contour feathers starts at same time as primary molt. Head-and nape-feathers are replaced first, followed by scapulars and rump-feathers. New head-and nape-feathers of light morphs are gray and soft; old feathers are brown and coarse. New scapulars have pale scallops at their tips, most conspicuous in light morphs in Dec. Light morphs in Dec also have gray vermiculations on crissum, flanks, and sides, similar to those of adult Pale-footed Shearwaters (*Puffinus creatopus*). In May, molt of contour feathers continues in scapulars

and on rump. After this molt, new plumage has brown gray upperparts. Mantle becomes increasingly browner with age ([King 1967](#)).

Some dark morphs captured at sea grow new primaries Jun–Sep; molt is complete by Oct. Other dark morphs molt from Nov to Apr. These discrepancies probably represent birds nesting in Southern Hemisphere (Phoenix Is., for example) and in n.-central Pacific, respectively, the 2 populations intermingling at sea ([King 1974](#)).

In dark morph, upperparts sooty brown; feathers of back and wings edged with lighter brown; primaries and rectrices black. Undertail-coverts black; chin, throat, and forehead brownish gray; remainder of undersurface dusky brown, rectrices become increasingly shorter from innermost to outermost feathers, producing distinctly wedge-shaped tail ([Oliver 1955](#), [Gross et al. 1963](#)).

Light morph is grayish brown above; has white underparts, dark undertail-coverts, and thick dark bands on under surface of wings near edges. Borders between light and dark areas are gray ([Munro 1967](#)).

Individuals intermediate between light and dark morphs; “masked white” breast gray ([Murphy 1951](#)).

Aberrant Plumages

Leucism rare, concentrated in head and neck and upper back; feet and legs pinker than usual ([Munro 1967](#), [Shallenberger 1973](#)).

Bare Parts

Bill And Gape

In Hawaiian Is., bill gray-brown; tip of bill darker. On Christmas I., most bills brown; one-third have whitish scaly discoloration on sides; a few have reddish brown bills ([Gallagher 1960](#)).

Iris

Light brown ring around central dark core ([Oliver 1955](#), [Gross et al. 1963](#), [Shallenberger 1973](#)).

Legs And Feet

Legs pearl gray, lead-colored ([Oliver 1955](#), [Serventy et al. 1971](#)). Feet flesh-colored; outer edge of outer toes darkly pigmented. Otherwise toes white ([Oliver 1955](#)). Outer toes stronger, thickened, and calloused, probably because of their greater use in digging ([Gross et al. 1963](#)).

Measurements

Linear

In Murphy’s ([1951](#)) compilation, body dimensions of *P. p. pacificus* are consistently larger than those of *P. p. chlororhynchus*. Largest birds appear to be in Kermadec Is., smallest in w. Indian Ocean. Only small differences between sexes; males generally slightly larger ([Table 1](#)). When members of pair are examined, however, head width, bill length, and nostril tip length are greater in male in 75% of cases ([Shallenberger 1973](#)).

Mass

- **Table 1.** *Body measurements (mm) and mass (g) of Wedge-tailed Shearwater on M&257nana I., off O‘ahu, HI. Data given as means ± SD (range; n). From Shallenberger 1973, except where noted. (*) From [Byrd et al. 1984](#), from birds measured at Kilauea Pt. on Kaua‘i Island, H*

Culmen	
Male	45.7 (43.3-50.5; 43)
Female	44.5 (42.3-47.0; 40)
Tarsus	
Male	50.2 (47.4-52.3; 30)
Female	49.9 (46.3-51.5; 28)
Wing	
Male	297.6 (285-305; 30)
Female	297.3 (288-306; 27)
Mass (*)	393.3 ± 30.7 (320-510; 113)

Priorities for Future Research

1. The designation of 2 subspecies is unsatisfactory because it has been challenged and the limited geographical distribution of one subspecies would seem to need confirmation.
2. There is a great need for satellite tracking of the migratory movements of individual birds and insight into the control and physiology of migration in this species.
3. There is a dearth of information on the immature stage.
4. Many details of breeding need to be filled in—for example, sex ratios and hatchling dimensions.
5. The diameter of the olfactory bulb of the brain is 30% that of the cerebral hemisphere—high compared with most species of birds, but about average for Procellariiformes ([Bang and Cobb 1968](#)). The role of olfaction in the biology of this species remains to be elucidated.
6. There is a paucity of information on the Indian Ocean population.

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