

Laysan Albatross

Diomedea immutabilis

FRENCH: *Albatros de Laysan*
SPANISH: *Albatros de Laysan*



The Laysan Albatross is a large seabird but a relatively small albatross, distinguished from most other species of albatross by its Northern Hemisphere distribution and its sub-tropical breeding range. It breeds mainly on atolls in the Hawaiian Archipelago during the northern winter, and outside the breeding season disperses into the North Pacific Ocean from July to November. Despite losing hundreds of thousands of breeders earlier this century to feather hunters and military development, this species has recently colonized new breeding grounds in the main Hawaiian Islands, the Bonin Islands, and off the Mexican coast. Estimates of the total population of this albatross now stand at about 2.5 million,

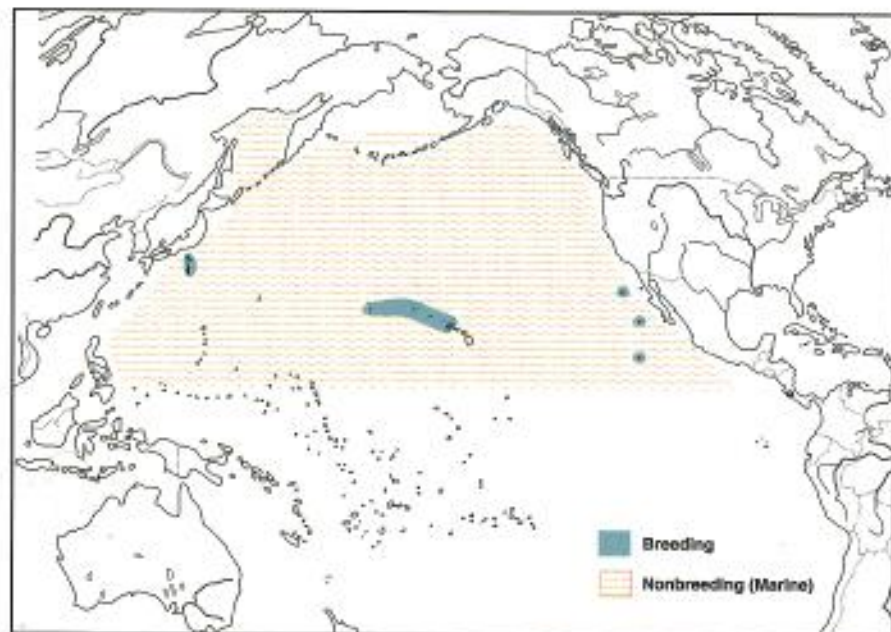
making it the most abundant species of albatross in the Northern Hemisphere and the second most numerous Hawaiian seabird.

The Laysan's mating dance is legendary and its method of flying ("dynamic soaring") is spectacular; in the absence of wind, however, it has difficulty in becoming airborne or landing. Although it does not breed until it is 8-9 years old, it is long-lived (individuals at least 40 years old have been identified) and capable of breeding every year.

The Birds of North America

Life Histories for the 21st Century

Figure 1. Breeding and nonbreeding (marine) range of the Laysan Albatross. See text for details.



Laysan Albatross feed mainly on squid, but fish, fish-eggs, and crustaceans are also taken. These seabirds feed mainly at night when squid are plentiful in surface waters and they are known to possess high levels of rhodopsin, a visual pigment that enhances nocturnal vision. At sea, Laysans are sometimes caught on fish hooks and in salmon and squid gillnet fisheries. Estimated loss to driftnets in 1990 was over 17,500 birds, nearly 1% of the total population.

DISTINGUISHING CHARACTERISTICS

Small albatross (79–81 cm long; wing span 195–203 cm; mean body mass = 2.4 kg, range 1.9–3.1; Harrison et al. 1983). Legs and webbed feet flesh pink. Bill pink with gray hooked tip. Head, neck, and underparts white. Upper wings and back dark sooty brown. Narrow white U-shaped area between dark upper rump and tail. Dark tail band visible during flight. Underwings have thick black leading edges and wing tips, and large black patches near the base within the central white areas. Gray-black patch in front of the eye extending as a thin line behind the eye. Sexes and juveniles similar. Distinguished from the Black-footed Albatross (*Diomedea nigripes*) by the uniformly sooty plumage of the latter. The other North Pacific albatross, the Short-tailed Albatross (*D. albatrus*), is much rarer, larger, with a heavier bill, and a yellow wash to the plumage on the back of the head and neck (Harrison 1990). Underwings of *D. albatrus* are all white and there is much white on the upper wings as well as on the back between the wings (King 1967).

DISTRIBUTION

AOU CHECK-LIST REGION

Breeding range. Breeding virtually confined to the Hawaiian Archipelago from Kure Atoll in the Northwestern Hawaiian Islands to Kauai in the Main Islands (Fig. 1). Attempts have been made to nest on Oahu, Molokai, Niihau, and Moku Manu in the Main Islands, but with little success (Harrison 1990), owing (in most instances) to active human discouragement because of danger to aircraft. In the mid-1980s a new colony was discovered on Guadalupe Is. off central Baja California (Dunlap 1988) and others are forming on San Benedicto Is. and Isla Clarion in the Revillagigedos, west of central Mexico (Pitman 1988, Howell and Webb 1989, 1992), and at Alijos Rocks, Mexico (Pitman 1985; Fig. 1).

Marine range. Recorded at sea between latitudes 8°N and 59°N and longitudes 170°E (which defines the westerly limits of the Am. Ornithol. Union region) and 105°W in the North Pacific Ocean (Thompson 1951, Fisher and Fisher 1972, Pitman 1985; Fig. 1). Seen regularly in Gulf of Alaska during northern spring and the s. Bering Sea in summer (Sanger 1974, Rice 1984). Birds are farther north in summer than during the breeding season (Sanger 1974) and nonbreeders concentrate near the Aleutians and in the Bering Sea. In recent years, found annually off California, mostly over deeper water well offshore; although records exist for every month, most numerous from late Oct to Feb (Stallcup 1990). At least 8 have been recorded inland in s. California and sw. Arizona, all during May-Jul; these were possibly northbound birds that became "trapped" in the n. Gulf of California and attempted to continue northward overland (McCaskie 1984, Rosenberg and Stejskal 1988).

RANGE OUTSIDE CHECKLIST REGION

A breeding colony is being established in the Bonin Is. (Ogasawara Is., 27°40'N, 142°07'E; Hasegawa 1978, 1984, Kurata 1978).

At sea, birds extend as far west as longitude 132°E (Fisher and Fisher 1972) and in summer penetrate the Sea of Okhotsk and the w. Bering Sea (Shuntov 1968). One sighting in Sea of Okhotsk in Dec (Shuntov 1974). Common in Jul, ESE of Kuriles (Kuroda 1955). In this region also, birds are farther north in summer (Sanger 1974).

HISTORICAL CHANGES IN DISTRIBUTION

Colonies on Johnston, Wake, and Marcus islands, and on the Izu Is., decimated by Japanese feather hunters at the turn of the century and have never recovered (Rice and Kenyon 1962a). Marcus once had an estimated population of one million birds (Rice and Kenyon 1962a). Midway and Laysan island (on Laysan I., more than 300,000 birds were killed in 1909 alone) populations also greatly reduced by feather hunters but have largely recovered. Lisianski population has remained depressed apparently because the vegetation was altered by introduced rabbits, destroying nesting habitat (Rice and Kenyon 1962a).

FOSSIL HISTORY

In the North Pacific Neogene (Miocene and Pliocene epochs, approximately 2.0–22.5 million years before present [mybp]), there are 3 extinct species in *Diomedea* and several more records for the genus (see Chandler 1990: 98). *D. californica* (Miller 1962: 471) and *D. milleri* (Howard 1966: 2) are both from the middle Miocene (late Barstovian North American Land Mammal Age [NALMA],

approximately 12 mybp) Round Mountain Silt, Sharktooth Hill Bonebed in Kern County, CA. Also middle Miocene in age are Albatross fossils from the Astoria Formation in Oregon (Olson 1985: 209). *D. howardae* (Chandler 1990: 96) from the San Diego Formation (late Blancan NALMA, 2.0-2.5 mybp), San Diego County, CA shares certain characters with *D. immutabilis*, but was larger.

SYSTEMATICS

GEOGRAPHIC VARIATION

No information.

SUBSPECIES; RELATED SPECIES

On the basis of differences in the bills, the Laysan Albatross has been allocated to one (*Phoebastria*) of three subgenera of *Diomedea* (Warham 1990).

Laysan and Black-footed albatross nest in close proximity; hybrids have been described (Fisher 1948, 1972, Ely and Clapp 1973). Fisher (1972) and Warham (1990) described hybrids trying to dance with Laysans but failing to complete the performance. Vocalizations ("Sky-moos") of the hybrids are intermediate in character between those of Laysan and Black-footed Albatross. No evidence for successful breeding by a hybrid, which also shows no interest in Black-footed. Hybridization supports the congeneric relationship between the two species and is in accord with the similar electrophoretic patterns in the blood proteins of the two species and the hybrid (Brown and Fisher 1966).

MIGRATION

NATURE OF MIGRATION IN THE SPECIES

Birds leave breeding islands to feed at sea.

TIMING AND ROUTES OF MIGRATION

Leave breeding grounds in Jul, heading northwest towards Japan (Shuntov 1974). Based on sightings and recovery of banded birds, they move northeast in Aug and then south towards the breeding islands in Oct (Fisher and Fisher 1972, Robbins and Rice 1974, Sanger 1974, see Fig. 3).

MIGRATORY BEHAVIOR

Homing ability to Midway was tested by Kenyon and Rice (1958). Longest return was made by a bird released in the Philippines, 6,867 km from Midway, and the fastest return was from

Washington State at an average speed of 581 km a day.

CONTROL AND PHYSIOLOGY OF MIGRATION

Arrive at the breeding grounds with heavy layers of fat (Fisher 1967) but lose 24% of their body mass between Nov and May (Appendix). Regain some of this mass before leaving in Jul, as the demands of feeding nestlings become less onerous. Wind is probably the most significant feature of the weather affecting distribution and movements (Sanger 1974). Albatross are incapable of sustained flight in calm air; equatorial Central Pacific waters thus represent an impenetrable barrier (Robbins and Rice 1974).

HABITAT

BREEDING RANGE

Sandy, grassy areas on low atolls. Prefers to be adjacent to shrubs such as *Scaevola*. See also Breeding: nest, nest site.

SUMMER MIGRATION

No special assembly or habitat.

MARINE RANGE

Jul to Nov at sea, never touching land but alighting on the water to feed and sleep. Most sightings seaward of continental shelf (McDermond and Morgan 1993). Found in waters between 2°C and 28°C and at air temperatures between -2°C and 26°C (Shuntov 1974). Prefers water temperatures between 4.4°C and 18.3°C (Fisher and Fisher 1972, Shuntov 1974). Habitat may be related to food distribution: feeds largely on squid, the distribution of which is tied to abundance of shrimp-like euphausiids (Fisher and Fisher 1972). Larger euphausiids occur in near-surface, eutrophic, cold waters (McDermond and Morgan 1993).

FOOD HABITS

FEEDING

Main foods taken. Squid, flying fish eggs, crustaceans, fish.

Microhabitat for foraging. See Migration: marine range. Incubating birds from Hawaiian colonies tend to be sighted nw. of the Hawaiian Islands; birds feeding nestlings closer to and ne. of these colonies (Fisher and Fisher 1972).

Food capture and consumption. Feed by sitting on the water and seizing prey. Use their powerful beaks to shred large prey. Scavenge natural carrion

or refuse from ships, but not as extensively as Black-footed Albatross does. Feed mainly at night; Laysans have high levels of rhodopsin, the visual pigment that enhances nocturnal vision (Harrison et al. 1983). Squid are more plentiful in surface waters at night than during the day; they possess light organs and migrate to the surface at night (Harrison 1990). Laysans often feed in flocks with other albatross but rarely with other species (Harrison 1990). Forage as far as 1,770 km away from the nest but, when tending nestlings, rarely go farther than a day's travel from the breeding grounds (Fisher and Fisher 1969). Intestine is long relative to wing length, to accommodate large intermittent meals (Kuroda 1986).

DIET

Major food items. Squid make up the bulk of the diet. Fish eggs constitute the largest fraction of the "fish" part of the diet, followed by sunfish (*Ranzania laevis*; Harrison 1990).

QUANTITATIVE ANALYSIS

Stomach contents, by volume: 65% squid (especially Ommastrephidae), 9% fish, 9% crustaceans, 4% coelenterates, and 10% stomach oil (Harrison et al. 1983). Squid were the highest ranked (according to number, volume, and frequency of occurrence in stomach samples) prey item, followed by flying fish (*Exocoetidae*), windsailers (*Velella velella*), and mysids (crustaceans). The length of Ommastrephidae ranged from 28 mm to 144 mm and that of Pyrosomatidae (pelagic tunicates), from 21 mm to 80 mm. Deep-water crustaceans are a puzzling dietary feature. For example, the amphipod *Eurythenes gryllus* occurs at depths down to 6,500 m. It may migrate to the surface at night or be carried to the surface attached to dead prey (Harrison 1990).

NUTRITION AND ENERGETICS

Pettit et al (1984a) modelled the energy requirements of the Laysan Albatross at French Frigate Shoals in the Northwestern Hawaiian Is. during the breeding season. From the energy requirements they estimated the food consumption necessary to meet these requirements. A population of 6,660 birds consumed 527 metric tons of food. This was the equivalent of 2.5×10^6 kilojoules of energy.

Total food consumption for the entire population of Laysan Albatross in the Northwestern Hawaiian Is. is 246,000–253,904 metric tons/yr (Whittow 1984a, Harrison and Seki 1987). Because of their size and numbers, Laysan Albatross account for more than half of the total consumption of fish, squid, and crustaceans by seabirds in the Hawaiian Is.

Energy expenditure of foraging birds is 2.6 times that of resting birds (Pettit et al. 1988). This is relatively low, probably because of the efficiency of their flight.

METABOLISM AND TEMPERATURE REGULATION

At Midway, resting oxygen consumption of birds averages $0.53 \text{ ml O}_2/\text{g hr} \pm 0.03$ (SE) with a respiratory quotient (RQ—ratio of carbon dioxide produced by metabolism to oxygen consumed) of 0.72, indicative of fat metabolism (Grant and Whittow 1983). Resting metabolic rate calculated from oxygen consumption is 83%–93% of predicted values for birds of their size, the exact figure depending on the predictive value used (Grant and Whittow 1983, Ellis 1984). Mean rectal temperature of ten incubating birds was 37.6°C ; that of ten non-incubating birds 39.4°C (Rice and Kenyon 1962b). Mean proventricular temperature of ten incubating albatross 37.5°C (Grant and Whittow 1983). Proventricular temperature measured by telemetry averaged $37.6^\circ\text{C} \pm 0.07$ (SE) over 27 d in one incubating male and $37.8^\circ\text{C} \pm 0.07$ (SE) over 12 d in another male (Grant and Whittow 1983). Mean body temperature of adults brooding nestlings under overcast conditions was 37.5°C during the day and approximately 1°C lower at night. Body temperature of birds that had been active in the sun was higher, about 40.5°C (Howell and Bartholomew 1961).

These birds pant (averaging 160 breaths/min) when exposed to heat but do not gular flutter (Howell and Bartholomew 1961). During heat exposure, rete mirabile ophthalmicum may keep their brain cool by countercurrent heat exchange (Pettit et al. 1981b).

Extensive array of behavioral responses to heat (Howell and Bartholomew 1961, Rice and Kenyon 1962b, Whittow 1980a): they partially lower themselves to balance on their heels and raise their large webbed feet off the ground. This permits convective cooling of the feet and reduces heat gain from the hot substratum. Also orient their bodies so that their feet are in the shade of their body. Scapular feathers are raised and the wings allowed to droop, both of which facilitate convective heat loss. Shade is sought and birds will stand on vegetation rather than warmer sand or soil.

DRINKING, PELLET-CASTING, AND DEFECATION

Observed to peck at falling rain drops (Frings and Frings 1959). During an incubation bout (up to 24 d), do not eat or drink and rarely defecate. Water loss during incubation is reduced by breathing moist air with the bill tucked under the feathers, and it is balanced by metabolic water production (Grant and Whittow 1983). Albatross,

like other marine birds, have salt glands above their eyes, connected by a duct to the nasal cavity. The glandular secretion, rich in salt, helps to get rid of the large amount of salt in the squid that they eat and any sea water that they may drink. Captive birds drink sea water (Frings and Frings 1959), and their salt glands become active after feeding on fish containing added salt. Before fledging, indigestible objects taken in with food (plastics, squid beaks, lenses, pumice) are regurgitated (Kenyon and Kridler 1969). Mean mass of these castings was 96.6 g (Pettit et al. 1981a).

FOOD SELECTION AND STORAGE

Ommastrephid squid preferred. Also pick up considerable quantities of floating pumice and plastic objects (Kenyon and Kridler 1969) which may be transferred to the nestlings during feeding (Pettit et al. 1981a, Grant and Whittow 1983). Plastics travel beyond the stomach to the intestine (Sileo et al. 1991). Floating plastics attract crabs, barnacles, and fish eggs, and flying fish may lay their eggs on floating plastics and pumice, so plastics may have some food value (Pitman 1988).

SOUNDS

VOCALIZATIONS

Development. No published information.

Vocal array. A number of distinctive sounds on the breeding grounds, many of them part of courtship display. Sounds described by Rice and Kenyon (1962b), and Meseth (1975) identified eight distinct vocalizations. On the basis of spectrogram analysis, Sparling (1977) described nine types of vocal sounds: Double Call (*Eh-eh*), Squeak, Whinny, Whines, Sky Call, Sky Moo, Grunts, Moans, and Inhalations. Spectrograms of harmonic *Eh*s may be used to distinguish between individual albatross (Sparling 1977). Although most frequencies are approximately 3 kHz, sounds as high as 32 kHz have been recorded (Sparling 1977).

Phenology. When the males return to the colony at the beginning of the breeding season they make Sky Calls.

Daily pattern of vocalization. No information.

Places of vocalization. Nonbreeding birds vocalize within the breeding colony and males vocalize from their home-base (Meseth 1975). At the nest site, during incubation, the parents "talk" to the egg with a three-syllable *Eh-eh-eh*.

Repertoire and delivery of songs. A representative sequence of sounds during the courtship dance (see Behavior: sexual) would be (Sparling 1977):

Table 1. Significance of Laysan Albatross vocalizations. After Sparling (1977).

SOUND	CONTEXT
<i>Eh</i>	Courtship, Agonistic
Sky call	Dance
Sky moo	Conflict
Squeak	Agonistic
Whine	Dance, Agonistic
Whinny	Courtship (given more by males)
Inhalations	Physical exertion
Moan	Physical exertion

BIRD 1: *Eh* Call, Whinny, *Eh* Call, Whinny, Whinny, Inhalation, *Ahh*.

BIRD 2: Whinny, Inhalation, *Ahh*, *Eh* Call, Whinny, Inhalation, Whinny.

Social context and presumed function of vocalizations. Table 1.

NONVOCAL SOUNDS

Sparling (1977) classified the bill sounds made by snapping the mandibles together or by two birds striking the sides of their bills together: Bill Snap—a single closure of the mandibles accompanying courtship, agonistic displays, displacement activities, and comfort movements; Bill Clap—a series of strikes separated by varied intervals occurring during greeting, dance, post-dance, agonistic behavior, and also during nibbling motions at the feathers; Bill Clackers—regularly spaced strikes during horizontal head and head-bowing posture; Clicks—rapid bill sounds during head shaking; rapping sounds during the dance—very soft.

BEHAVIOR

LOCOMOTION

Walking, hopping, climbing, etc. Characteristic plodding walk. After landing they walk to their nests. At the breeding grounds some birds, probably nonbreeders, walk around the colony. Entirely terrestrial; never land on trees or shrubs.

Flight. Need wind for flight. Long narrow wings facilitate "dynamic soaring," taking advantage of the gradation of wind velocity at different heights above the surface of the water. "Slope soaring" makes use of the wind deflected upwards from the windward face of a wave (Warham 1990). The two processes are combined in a spectacular flight sequence, the bird skimming the surface at high speed across the wind, a wing tip often cleaving the water, then soaring upwards into the wind. At the top of its climb, the albatross banks to leeward

and descends rapidly downwind. The sequence is repeated over and over, with only an occasional flap of the wings, resulting in effortless, graceful flight.

Depending on wind strength, take-off may be difficult, requiring a long run with the head outstretched, the bird flapping its wings and literally running. Take off from water is similar, requiring furious paddling with the webbed feet. Landings can be equally difficult especially in birds that have been at sea for months, or in light winds. In the absence of the braking effort of a strong wind, landing birds may literally tumble head over heels on landing. Birds returning to their breeding island often fly in small groups just above the horizon.

Swimming and diving. Settle on the water to feed, especially at night. May dip head and bill into the water, and occasionally the entire body. Webbed feet are important propulsive organs during take off. Spend less time afloat than does the Black-footed Albatross (Palmer 1962).

SELF-MAINTENANCE

Preening, head scratching, stretching, bathing, anting, etc. Do not bathe in fresh water ashore. Anting not seen. Mouthing or mutual preening performed from sitting position (Rice and Kenyon 1962b). One bird gently nibbles the other bird on the head.

Sleeping, roosting, sunbathing. Do not sunbathe but display thermoregulatory behavior in response to heat stress in their tropical and subtropical breeding colonies. Do not roost. Sleep with bill tucked under scapulars.

AGONISTIC BEHAVIOR

In general, individuals tolerate neighbors. Even in densely populated areas, nests are far enough apart to permit a bird to walk between them without being pecked by sitting birds. Agonistic behavior, when it occurs, may be directed at nestlings in adjacent nests. This achieves the same result: if the nestling dies its parents may not breed at that nest site the following year (Harrison 1990).

SPACING

Males actively defend an area, termed "home base" by Meseth (1975) and established in earlier visits to the colony, and solicit passing females from it. Pairs return to the same home base for the duration of their bond. Territorial activities change to the nest site after its establishment by the female. Fifty percent of pairs construct their nests within 1.3 m of the previous year's site; none move more than 6 m (Rice and Kenyon 1962b).

In defense of the nest the male is the more aggressive, but prelaying females will attack any other female within reach (Fisher 1971a). Bill thrusts are the primary defense. While preparing nests, females may grab each other's bills and a tug of war may ensue (Fisher 1971a). Will not leave the nest while incubating or brooding to attack an intruder, so at this time defense consists of snapping at an intruder (Rice and Kenyon 1962b).

SEXUAL BEHAVIOR

Mating system. Monogamous. Males start breeding 1 yr earlier than females; mean age 8.4 yr in males, 8.9 yr in females (Fisher 1975a, Van Ryzin and Fisher 1976); 90% of pairs had 4 or fewer partners over a 9 yr period (Fisher 1976). Changing mates results in decreased breeding frequency. In Fisher's colony at Midway, most of the breeding birds were > 15 yr old and only 15% were 9 yr or less (Fisher 1976).

Pair bond. Forms over several years. Birds may return to their breeding island when 3 yr old but not nest until 7 or 8. Pair bond is established by ritual dancing and remains intact until broken by death or disappearance of partner. Ritual display is elaborate, consisting of 25 different postures (Meseth 1975; Fig. 2); in the dance these tend to be grouped into four sets. Sparling (1977) describes the sequence of sounds in the two dancing birds and the variations in sequence between different pairs (see also Vocalizations; Table 1). The dance may involve a third bird. Dancing begins with the arrival of the birds at the breeding grounds but only pairs breeding for the first time and nonbreeders dance (Meseth 1975). Nonbreeding birds continue to dance during the breeding season. Dance is completed only by birds of the same species. Males require their mates to be shorter, with shorter bills (Fisher 1972) so that the breast, which is the largest and most obvious part of the male's body, is at the level of the female's head (Fisher 1972). In 85% of the cases, dances are performed between birds of the opposite sex (Frings and Frings 1961).

Copulation. Males arrive back in the colony first; experienced pairs may copulate within 24 hr of the arrival of the female (Fisher 1971a). Female adopts a submissive posture with spread wings and bent head; male places its bill over the back or neck of the female (Fisher 1971a). Copulation is subdued, lasts 2 to 3 min, and is never interrupted by adjacent males. Afterwards, the birds circle the site, bill-touch, mutual-preen, and utter *Eh ehs*. Within 2-5 h, the two birds depart for the sea where they remain for about 8 d (pre-laying exodus). Copulation occurs 8-10 d before the egg is laid (Fisher and Fisher 1969). Male rarely copulates with female other than his mate;

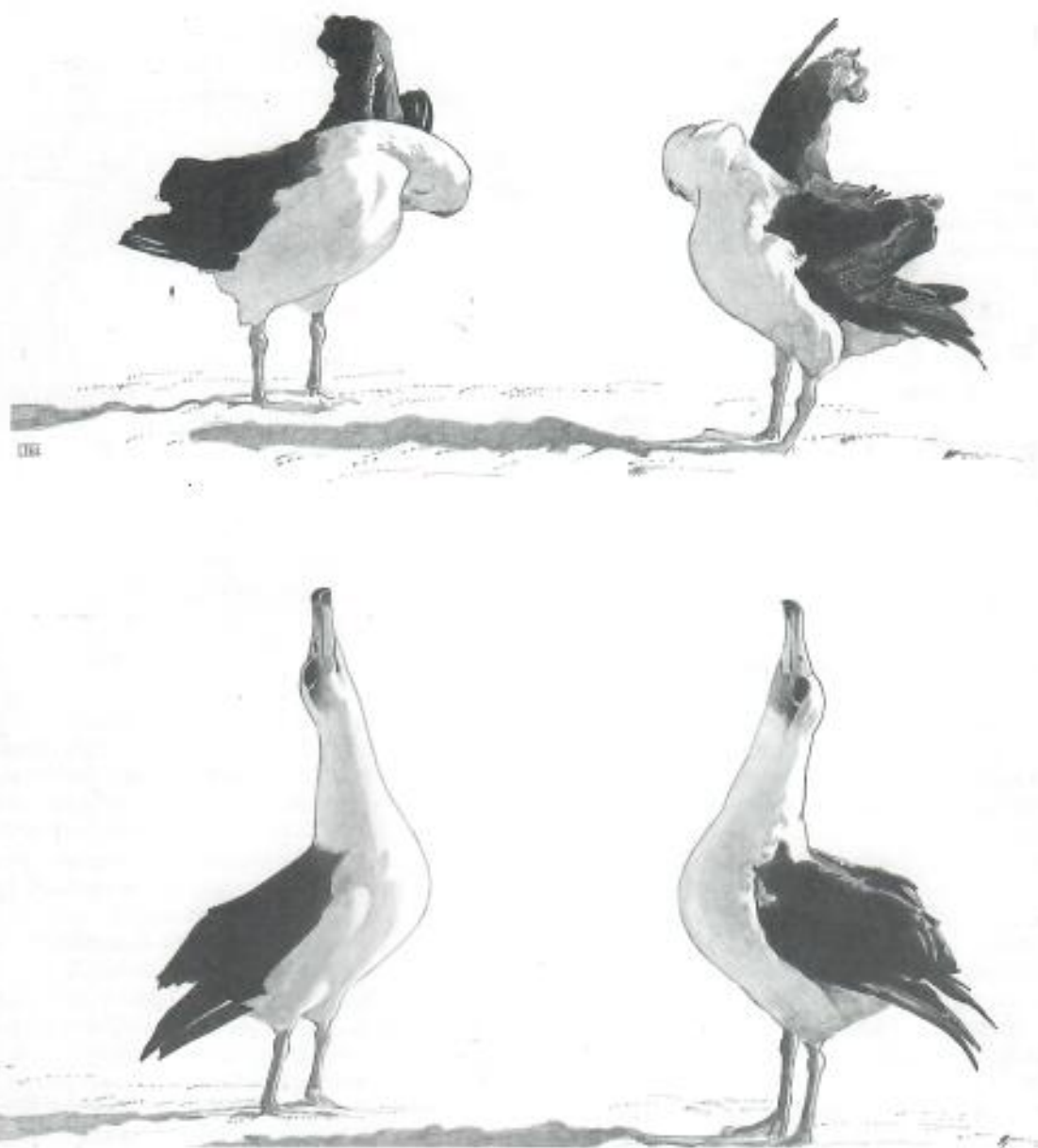


Figure 2.

Adult Laysan Albatross performing two components of their elaborate courtship dance. Top: Bill Under Wing Stance; Bottom: Sky Call. Drawings by D. Otto, from photos by M. J. Rauzon/VIREO.

nonbreeders may copulate occasionally but birds < 6 yr of age seldom do so. Rape occurs but apparently does not result in insemination (Fisher 1971a).

SOCIAL AND INTERSPECIFIC BEHAVIOR

Colonial nesters. Dances with sympatric Black-footed Albatross (*D. nigripes*) but the dance is never completed. The existence of hybrids, however, is proof that the two species can mate.

PREDATION

Only known predators are tiger sharks (*Galeocerdo cuvieri*) which prey particularly on

fledglings leaving the breeding islands. Incidence of one-legged adults suggests attacks by predatory fish (Harrison 1990). Polynesian rats (*Rattus exulans*) occasionally attack incubating adults on Kure Atoll (Kepler 1967).

BREEDING

PHENOLOGY

From Rice and Kenyon (1962b), Fisher and Fisher (1969), Fisher (1969)—all studies on Midway.

Pair formation. Experienced birds begin to arrive at the breeding colonies at Midway on 1 Nov. Males usually arrive at the breeding grounds 8 d ahead of the females. First-time breeders usually arrive in the last week of Nov and first week of Dec. Younger birds arrive back progressively later, depending on their age, and 1 yr olds do not return to the breeding islands. Following copulation, both sexes participate in the pre-laying exodus (see Breeding: sexual behavior). Females return first and 50% are alone when the egg is laid.

Percentage of experienced birds that breed annually varied from 44% to 100% over a 12-yr period (Fisher 1969, 1976). Low percentages were apparently due to poor food availability; 99% of birds that lost their partners did not attempt to breed the following year. Changing partners also reduces the percentage of seasons in which breeding takes place. Sixty percent of birds breeding for the first time do not breed the following year.

Nest building. After returning from the pre-laying exodus the female begins construction of the nest, although some nests persist from one season to another. Nest building begins only 1–3 d before the egg is laid.

Egg laying. Only 1 egg/yr; if destroyed, not replaced. Eggs are laid from mid-Nov to mid-Dec at Midway (Fig. 3). The median date of experienced breeders is a week earlier than that of females laying for the first time.

Hatching. Eggs hatch from 22 Jan to 19 Feb (Rice and Kenyon 1962b, Fisher 1971a; Fig. 3).

Fledging. Averages the middle of Jul (Fig. 3).

Departure. Successful breeders begin to depart in mid-Jun and most have gone by the last week in Jul (Fig. 3).

Nov-Jul breeding. Nesting cycle corresponds to the southern-hemisphere summer, when most other species of albatross breed. Rice and Kenyon (1962b) considered the winter-breeding to be an adaptation to its sub-tropical climate rather than an inherited endogenous rhythm from its distant ancestors. Harrison (1990) believed that Laysan Albatross breed in the northern winter because their food is more plentiful then and longer nights are an advantage to a nocturnally feeding species.

NEST SITE

Ground, on grass or sand, preferably close to tall vegetation.

NEST

Construction. Nests formed by the female squatting in a depression, lying on one side, and scraping sand backwards with feet and claws, rotating constantly. Twigs, leaves, and sand are dragged back to form a rim. Rim protects the egg

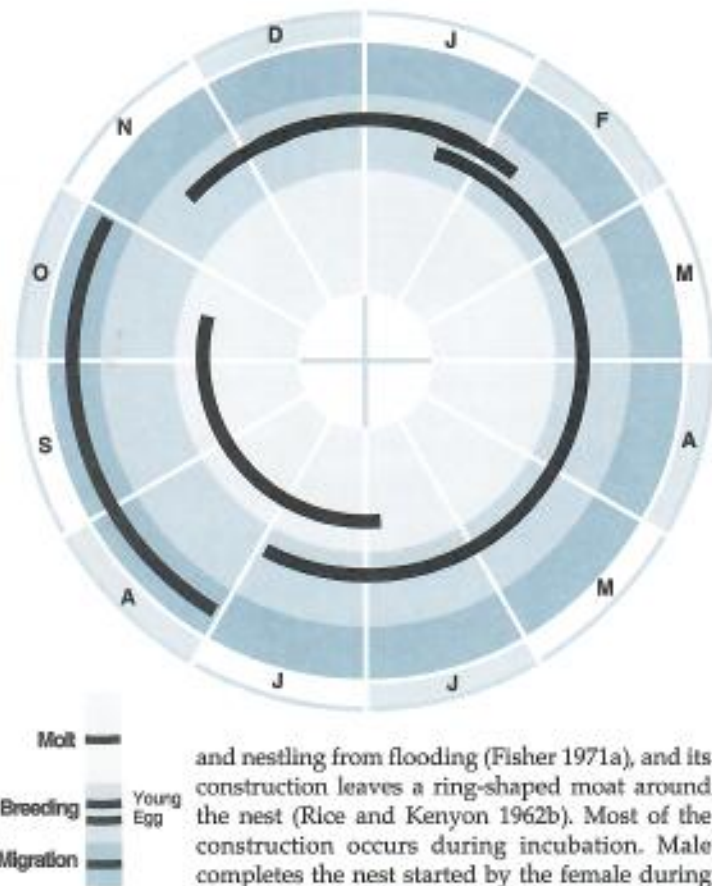


Figure 3. Annual cycle of Laysan Albatross breeding, molt, and migration, Northwest Hawaiian Islands. See text for details.

and nestling from flooding (Fisher 1971a), and its construction leaves a ring-shaped moat around the nest (Rice and Kenyon 1962b). Most of the construction occurs during incubation. Male completes the nest started by the female during his first incubation span making extensive use of his bill. Improvement of the nest continues throughout incubation but lessens towards hatching (Fisher 1971a).

Structure. Essentially a depression in the sand or soil with a rim of variable height.

Dimensions. Diameter of nest and moat 99 cm (Frings and Frings 1961), 86–102 cm (Fisher 1971a). Moat may be up to 5 cm deep (Rice and Kenyon 1962b). Height of the rim is usually less than 20 cm but may be as high as 25 cm (Fisher 1971a).

Maintenance. Maintenance ceases with hatching. Nestling's scraping may lower the floor of the nest bowl (Fisher 1971a).

Nest density. Mean distance apart (edge to edge) of neighboring nests on Midway 66 cm (Frings and Frings 1961). Nest densities highest (4.2 m²/bird) on "strips of edge" (Fisher 1966b) and near buildings (6.5 m²/bird; Frings and Frings 1961); lowest (134.7 m²/bird) in open areas with scattered grass (Frings and Frings 1961).

Nonbreeding nests. During the guard stage, when an adult remains with the nestling (Rice and Kenyon 1962b), nestlings frequently build a miniature nest of their own adjacent to the original nest and, after the guard stage, nestlings may build an additional nest within 30 m of the original, often in the shade (Rice and Kenyon 1962b). Nests

are often built by nonbreeding pairs or by birds "keeping company."

EGGS

Shape. Ovate or elliptical ovate.

Size. Length: 107.6 mm \pm 0.3 (SE; $n = 105$); breadth: 68.6 mm \pm 0.2 (SE; $n = 105$); mass: 284.8 g \pm 1.9 (SE; $n = 88$); volume: 267.6 ml \pm 3.2 (SD; $n = 36$, Grant et al. 1982b). Grant et al. used a large sample of eggs and substantiated their value for fresh-egg mass by replacing air[cel] gas with distilled water in other eggs. Eggs of older birds are larger than those of younger females (Fisher 1971a). Fresh-egg mass represents 9.5% of the body mass of the adult female on her arrival at the breeding colony. Mean egg density of 36 eggs was 1.074 g/ml \pm 0.001 (SE) and the calculated surface area was 204.8 cm² (Grant et al. 1982b).

Egg composition. Contents represent 92.7% of the mass of the freshly-laid egg (Pettit et al. 1984b). Water amounts to 74.2% of the egg contents. Yolk/albumen ratio is 0.50 and the total energy content of egg is 1891 kJ. Larger eggs are mainly associated with greater amounts of albumen rather than shell or yolk (Warham 1990).

Eggshell thickness. Shell thickness (including the shell membranes) of 42 eggs on Midway 0.491 mm \pm 0.009 (SE; Grant et al. 1982b); calculated shell volume and density were 10.06 ml and 2.05 g/ml, respectively. Measurements taken after the introduction of DDT in 1947.

Eggshell mass. No decrease in eggshell mass between 1910 and 1982 (Fisher 1973, Grant et al. 1982b). Mean shell mass of 42 eggs on Midway was 20.61 g \pm 0.32 (SE; Grant et al. 1982b).

Color. Eggs are creamy white with brown spotting and a cap of reddish brown on the blunt end of the majority of eggs (Frings 1961). Brown color is due to blood from the oviduct.

Texture. At first the surface is smooth but as incubation proceeds the surface becomes chalky white and rough (Fisher 1969).

Egg laying. Interval between the arrival of the first birds at the breeding colony and the laying of the first eggs is 14–16 d (Rice and Kenyon 1962b). Older birds that remate also lay later. One percent of nests have 2 eggs in them, the second egg being laid by another female; 3.4%–9.8% of eggs laid are infertile (Fisher 1971a).

Female adopts a drooped-wing posture during extrusion of the egg (Rice and Kenyon 1962b). Egg is extruded pointed end first; takes 11–73 min to lay the egg (Fisher 1969). Most birds lay during the day, 66% before 10:00 (Fisher 1969). Only one egg is laid each season (Fisher 1968, 1969, Rice and Kenyon 1962b); females capable of laying an egg each year, although 30% of former breeders may not breed in any one year (Fisher 1969).

INCUBATION

Incubation in relation to laying. Incubation starts immediately after the egg is laid.

Incubation patch. Both sexes develop an incubation patch (Rice and Kenyon 1962b, Fisher 1971a). Loss of down feathers leaves a cavity averaging 50 x 95 mm. Because of its sac-like nature Fisher (1971a) referred to it as a "pouch"; it accommodates the single egg so tightly that the egg remains within the pouch when the bird stands. However, Grant et al. (1982b) reported that the measured incubation patch area (48.7 cm²) represents only 24% of the egg surface area (204.8 cm²). Skin surface temperature of the patch is 36.7°C, 0.8°C lower than deep-body temperature during the day, and 0.7°C higher than egg temperature (Howell and Bartholomew 1961). In some experienced breeders the patch begins to develop before they return to the colony and it develops about a week earlier in breeding males than in females (Fisher 1971a). Patch is always complete before the egg is laid. Reforeathering of the patch begins in some incubating birds in mid-Jan (i.e. before the end of incubation), and most breeding birds have no patch after 1st Mar. Patches are not seen in birds < 4 yr old.

Incubation period. Mean incubation period 64.4 d \pm 1.0 (SD; $n = 95$; Rice and Kenyon 1962b). This is longer than expected for most birds (Whittow 1980b) but not for Procellariiformes (Rahn and Whittow 1988). Eggs of experienced birds, laid early in the season, average 65.6 d; eggs of inexperienced birds, laid later, average 63.8 d (Fisher 1971a). Adults can incubate only one egg (Rice and Kenyon 1962b).

Egg mass loss. Eggs lose mass continually during incubation; average daily loss of mass (\pm SE) in 98 eggs: 0.674 g/d (Grant et al. 1982b). Mass loss greatest in piped eggs, 8.8% of the total mass loss occurs after the eggs pip (Pettit and Whittow 1983). Mass loss is due to loss of water from the egg; total water loss during incubation represents 16% of the mass of the freshly-laid egg (Pettit and Whittow 1983).

Embryonic growth. Growth of the embryo during incubation described by a logistic growth curve (Pettit et al. 1982). Muscle grows fastest (Zhang and Whittow in press). Compared with other Procellariiformes, the energy cost of embryonic growth is not high (Whittow 1984b).

Parental behavior. Incubation is continual and both sexes share incubation duties (Rice and Kenyon 1962b). First incubation span by the female lasts 2.1 d, on average (Fisher 1971a). Experienced females remained on the egg for 1.7 d; inexperienced females for 3.0 d. Second incubation span, by the male, 24.1 d (living off fat). Subsequent spans are shorter; usually five spans needed to

complete incubation. Egg may hatch while either male or female is incubating. Total amount of time incubating is greater for males (36 d) than for females (29 d; Fisher 1971a). If not relieved, either parent may remain on the egg for as long as 58 d (Fisher 1967).

Exchange of birds at the nest usually occurs in daylight, preceded by mutual preening and rest periods. Relieving bird may try to put its bill across the neck of the incubating bird. When the incubating bird stands its mate pushes it off the nest. Relieving bird then *eh-eh*'s to the egg. Relieved bird circles the nest, picking up debris and tossing it rearwards (LeFebvre 1977). Most relieved birds depart the nest within an hour of being relieved.

Incubating birds may lose a considerable amount of body mass, up to 22% during a long incubation span (Rice and Kenyon 1962b). To stay alive, must maintain body mass of at least 1,600–1,900 g (Fisher 1967).

Fisher (1971a) reported that incubating birds forcefully defecate beyond the rim of the nest. This must occur at the beginning of the incubation shift because Fisher also states that, after several days at the nest, the digestive tract is empty; Grant and Whittow (1983) reported that incubating birds do not defecate.

Energy expenditure of incubating birds is similar to that of resting birds not incubating (Grant and Whittow 1983, Grant 1984, Pettit et al. 1988); i.e. there is little energy "cost" to incubation for the incubating bird. Overall energy expenditure of the female during the incubation period is greater than that of the male because the female spends more time foraging at sea.

Incubating bird rises from the egg approximately 1.4 times/h (Grant et al. 1982b). This "nest ventilation" results in transient decreases in incubation patch temperature and also in a flushing of moist air surrounding the egg. Standing up and flapping the wings was the most effective nest ventilation behavior.

Adults do not attempt to retrieve a displaced egg; they choose to return to the empty nest rather than the displaced egg (Bartholomew and Howell 1964). They will incubate a variety of foreign objects but, given a choice, will choose an egg.

Fisher (1971a) reports: (1) Incubating birds look at the egg and also "talk" to it, uttering 2 to 4 *Eh-ehs*. (2) When an intruder enters the colony, the nearest birds will sound a "mild alarm note" in which they clack their bills softly. (3) Undisturbed birds make a soft click. (4) Incubating birds indulge in "nonsense behavior," tearing up anything within their reach.

Egg temperature; hardness of eggs. Central egg temperature increases during incubation, from

34.2°C on 2 Dec to 37.3°C on 21 Jan (Grant et al. 1982b). Howell and Bartholomew's (1961) figure of 36.0°C for the mean egg temperature of "advanced" brooded eggs falls within this range. Egg is incubated continually; eggs chilled for several days, however, still hatch (Fisher 1971a).

HATCHING

Preliminary events and vocalizations. Initial event in the pipping period is penetration of the aircell by the embryo's beak (internal pipping). It permits the embryo to use its lungs to rebreathe the air in the aircell and it also allows the embryo to vocalize ("peep"). This event occurs 4.5 ± 0.9 (SD) before hatching (Pettit et al. 1982).

Shell breaking and emergence. Star-fracture of the shell (external pipping) takes place 3.5 ± 0.8 (SD) before hatching (3.23 ± 0.65 according to Rice and Kenyon 1962b); this is followed by the formation of a distinct pip hole 2.4 ± 0.6 (SD) before hatching (Pettit et al. 1982).

Adults do not aid in hatching and do not dispose of the eggshell, which is trampled into the nest (Fisher 1971a). No particular time of day favored for hatching (Fisher 1971a).

YOUNG BIRDS

Condition at hatching. Hatchlings downy; eyes open. Mass of 50 hatchlings at Midway: 190 g \pm 10.2 (SD, Fisher 1967), including 22.8 g of yolk (Pettit et al. 1982).

Wing approximately 35 mm, middle toe 36 mm, culmen 33 mm, and tarsus 21 mm (Rice and Kenyon 1962b).

Covered with gray, white-tipped down giving the hatchling a peppercorn appearance (Rice and Kenyon 1962b). Golden tinged around neck; down is longest on the dorsum, shortest on wings (Dawson and Whittow in press). Bill and feet dark blue-gray with pink tinge. Mass-specific oxygen consumption of the hatchling is 45% higher than that of the adult (Grant and Whittow 1983, 1984) and hatchlings have higher body temperatures than do adults (Howell and Bartholomew 1961). Body temperature of hatchlings with wet plumage diminishes more rapidly than in hatchlings with dry plumage (Howell and Bartholomew 1961). Hatchlings respond to lowered environmental temperature with increased metabolic rate and, in this way, attenuate the decrease in their body temperature (Dawson and Whittow in press).

On the basis of the yolk, caloric, and water content of the egg, classified as semi-precocial in terms of the maturity of the hatchling (Pettit et al. 1984b), and the down covering and thermo-regulatory response to cooling is in accord with this designation.

Hatchling remains at the nest where it is fed by the parents.

Growth and development. Data obtained by Rice and Kenyon (1962b), Fisher (1967), and Grant and Whittow (1984) at Midway show a rapid increase in nestling mass during the first 10 d after hatching followed by a more gradual increase. Body mass attains a maximal value (3.18 kg) at 112 d post-hatching and declines thereafter to 2.3 kg when they leave the colony, and 2.0 kg when they leave the island. Nestlings with large amounts of ingested plastics in their proventriculi had lower fledging body mass than did those with low amounts (Sievert and Sileo in press).

The middle toe, culmen, and tarsus grow linearly with time until day 75 (when measurements ceased; Rice and Kenyon 1962b). Growth of the wing during the same time period is more exponential, the growth accelerating with time. No published data for linear dimensions of the body parts beyond the 75th d.

After hatching, the mesoptiles begin to grow, the protoptiles remaining attached to their tips. By the end of the guard stage (see below) nestling is covered with the long dense secondary down (Rice and Kenyon 1962b) which is slightly darker (Palmer 1962). Primaries begin to sprout at approximately 35 d of age. Mesoptiles remain firmly attached until late Apr or early May. Down is first lost from the back and sides, then from the abdomen; upper breast, neck, and head are the last areas to lose their down; head may retain some down at fledging.

Body temperature of nestlings (39.3°C) exposed to intense solar radiation was higher than that (37.2°C) of sleeping nestlings at night (Howell and Bartholomew 1961). Nestlings have an impressive repertoire of thermoregulatory postures and behaviors documented by Howell and Bartholomew (1961), Rice and Kenyon (1962b), and Whittow (1980a): (1) They seek shade, walking as much as 26 m from the nest site but always returning to the nest site in the evening. (2) They rest on their heels (tibio-tarsal joints) and raise their webbed feet 3–10 cm above the surface of the ground. This allows them to avoid contact with the hot substrate while permitting convective cooling from both surfaces of the feet. Effectiveness of this posture is enhanced by the nestling's orientation so that their feet are in the shade of their own bodies. Their pear-shaped bodies have centers of gravity that facilitate this posture more so than in the adults. Foot temperature (36.3°C) is higher than that of the air (29.4–31.0°C) but lower than that of the substrate (39.5–40.2°C). Skin of the webbed feet is very vascular. (3) Nestlings scoop away the surface layer of substrate in their nest pits, thus exposing cooler material beneath. (4)

They may sit on the elevated rim of the nest, where there is more air movement. (5) They droop their wings, thereby promoting convective heat loss. In addition to these manifestations of behavioral thermoregulation, nestlings can increase evaporative cooling by open-mouthed panting (Howell and Bartholomew 1961, Rice and Kenyon 1962b); panting rates may be as high as 198/min (mean = 160/min).

Oxygen consumption increases with age, reaching adult levels at or above approximately 75 d of age (Grant and Whittow 1984). During this period, mass-specific oxygen consumption diminishes while the respiratory quotient averages 0.78, indicative of the metabolism of a diet consisting of a high proportion of fat and protein.

For the first few days, the nestling is inactive. During the guard stage (i.e. while a parent is still in attendance), the nestling may build its own miniature nest beside the original nest (Rice and Kenyon 1962b). While the parents are absent, the nestling may wander as far as 30 m from the nest but always returns to the nest site to be fed. Adult will not feed its nestling until it returns to within a few meters of the nest site. Older nestlings recognize their parents, running up to the parent and begging for food. Prior to departure from the nest, young birds strengthen their wings for several weeks by spreading them in the breeze, flapping (Pettit et al. 1981b), and making short flights of a few meters.

Polynesian rats (*Rattus exulans*) prey upon nestlings at Kure Atoll (Woodward 1972) but the larger roof rat (*Rattus rattus*) does not seem to prey on Laysan Albatross at Midway (C. S. Harrison pers. comm.).

One-month-old nestlings exchanged between nests on different islands tended to return (at the age of 4.5 yr) to the island from which they had fledged rather than the site at which they had hatched (Fisher 1971b).

PARENTAL CARE

Brooding. Brooded by the parent for the first few days, after which the head protrudes from under the adult's wing, breast, or tail (Rice and Kenyon 1962b). When it is too large to be brooded, one of the parents sits beside the nest and guards it. Male and female share equally in guarding the nestling. Guard spans are much shorter than incubation spans; longest recorded span is 6 d. On average, nestlings are guarded continuously for 17.2 d after hatching, with a range of 12.0 to 24.5 d. After the nestlings are left unattended for the first time, they are guarded intermittently for another 10 d (Rice and Kenyon 1962b). Up to about 10 d after hatching, parents do not recognize their own nestlings (Rice and Kenyon 1962b). Body

temperature of brooding adults (mean = 37.5°C) during the day is almost 1°C higher than that of brooding adults at night (Howell and Bartholomew 1961). Adults shade nestlings from intense solar radiation by standing over them (Whittow 1980a).

Feeding. During the post-guard stage the parent bird visits the nestling only briefly to feed it. Nestling is fed by regurgitation stimulated by nibbling at the adult's bill (Rice and Kenyon 1962b). Nestling inserts its bill crosswise between the adult's mandibles allowing the ejected oil and partially digested stomach contents to pour into its throat. During a single visit lasting 15–25 min, nestling may be fed 3–4 times. Prior to feeding, the nestling makes the begging "peep-peep" call. After feeding its nestling, adult often rushes to the nearest neighboring nest and attacks the unattended nestling. Attacking adult gives a high-pitched shriek and approaches the nestling with its head lowered and neck extended. Nestling being attacked exhibits facing-away behavior. Attacks may ultimately lead to the death of the nestling.

Pettit et al. (1984b) calculated that a hatchling could subsist on its yolk reserve for 4.4 d were it not fed. However, during the first 2 wk after hatching, the nestling is fed, on the average, every 0.88 d. When the nestling is guarded intermittently, the mean feeding interval is longer—1.42 d. After that, the mean interval increases to 2.46 d. The greatest recorded distance traveled by a Laysan Albatross in a day is 528 km (Kenyon and Rice 1958). Thus, the farthest from the nest that an albatross might travel in 2.46 d would be 650 km. Nestling is usually fed during the day.

For the first few days after hatching, nestlings are fed stomach oil exclusively; such oil also forms a large proportion of the diet of older nestlings. This is consistent with the low respiratory quotients (RQ) of nestlings because the metabolism of fats and oils results in a low RQ (Grant and Whittow 1984). The oil is derived from the adult's food and it represents an efficient method of storing energy nutrients in the adult's body for delivery to the nestling. By 6–7 wk post hatching, most nestlings are recognized by their parents who will not feed an unfamiliar nestling (Rice and Kenyon 1962b). A breeding pair cannot rear more than one nestling and a single parent cannot rear one nestling (Rice and Kenyon 1962b). Fisher (1967) weighed adults during the nestling period and found that their body mass fell until the nestling reached its maximal mass, and then rose (Appendix).

Nest sanitation. Nest is kept clean because the nestlings eject the feces in a forceful stream a meter or more beyond the nest (Rice and Kenyon 1962b). In general, the amount of feces is small.

Nest defense. During the guard stage, as during incubation, the adult bird will snap at intruders.

Nest site tenacity. Adults do not attempt to retrieve a displaced nestling; adult will choose the nest rather than a displaced nestling (Bartholomew and Howell 1964). Nestlings removed from their nests are ignored by their parents (Rice and Kenyon 1962b).

COOPERATIVE BREEDING

Nonbreeders will sit on an uncovered egg. LeFebvre (1977) described an abandoned nestling that was fed successfully by 6 other adult birds.

BROOD PARASITISM

None

FLEDGLING STAGE

Departure from the nest. Nestlings may be fed on their last day at the nest but the amount of food is inadequate. Departure may be stimulated by hunger. Fledglings leave the Midway colonies from 20 Jun to 2 Aug, but most leave between 5–25 Jul (Fisher and Fisher 1969, Fig. 3). Departure from the island itself may take place 2–3 d later, the birds moving towards the beach and making trial flights over the lagoon (Fisher 1967). They then fly northwest to the ocean east of Japan (Robbins and Rice 1974).

Period from hatching to departure. Mean = 165 d (Rice and Kenyon 1962b).

Condition of development at departure. Apart from tufts of down on the head, the fledglings are almost identical in appearance to adults. There may be a few grayish feathers on the upper thighs and gray flecks on the crown, while the bills are gray-black, distinguishing them from the adult (Rice and Kenyon 1962b). They leave the island at body mass of 2 kg, well below that of breeding adults at the same time (Appendix).

Association with parents or other young. Fledglings tend to leave at the same time as their neighbors (Fisher and Fisher 1969). They move in the direction of the reef and open ocean rather than the lagoon at Midway.

Predation. Fledglings fall prey to sharks as they swim away from their nesting islands (Fisher 1975b). Tiger sharks may kill 1 fledgling in 10 in Jul (Harrison 1990).

Ability to get around, feed, and care for self. Fledglings have to learn to swim, fly, and feed. Some leave the nest site too soon: Rice and Kenyon (1962b) found emaciated nestlings along the beaches—birds that had left the nest site before they were effective fliers and were no longer being fed. Most of them died.

IMMATURE STAGE

Do not return to breeding colonies until the 3rd yr after hatching (Rice and Kenyon 1962b). At sea

during this period (Fisher and Fisher 1972). During their first summer and autumn, young remain south of the adults (Robbins and Rice 1974) and in winter closer to Japan. Japanese region is a nursery foraging area for birds < 4 yr old. In their next 4 summers, young move north-northeast away from Japan. Most fledglings moved experimentally from their natal breeding ground on Sand I. (Midway) and released on Eastern I. (also Midway; 4.7 km distant) were recaptured at age 4.5 yr (before breeding), and age 8.5 yr (breeding), on their natal breeding ground at Sand I. (Fisher 1971b). Similarly with fledglings moved to Lisianski I., 443 km from the natal site.

LENGTH OF THE BREEDING SEASON

Total length of the breeding season from the time of arrival of the adults to their departure after breeding is 290 d.

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY

Age of first breeding; intervals between breeding. Average age at which breeding begins is 8.4 yr for males and 8.9 yr for females (Fisher 1975a). Most birds breed annually; 76% of breeders successful in fledging a nestling return to attempt breeding the following year (Fisher 1976). In the first 5 yr of the pair bond between inexperienced birds, reproduction is attempted in only 59% of the seasons, and more than half of these young pairs do not attempt to breed the next season (Fisher 1976).

Clutch size. Only 1 egg/clutch and only 1 egg/yr.

Annual and lifetime reproductive success. Hatching success (eggs hatched/eggs laid) at Midway averages 64% but may be as low as 55% in a bad season (Fisher 1971a, 1975b). Desertion is the main cause of egg loss. Failure of the mate to return is the most important cause of desertion of the egg (Fisher 1971a). Most desertions occur during the early days of long incubation spans. The two sexes are equally likely to desert; some individuals are especially prone to desertion. Inexperienced breeders desert more often than experienced ones.

Fledging success (birds fledged/eggs laid) also averages 64% on Midway (Fisher 1975b, but 54.4% on Kure, Woodward 1972) but there is wide variation (range = 49%–78%) and calculations based on Fisher's (1975b) data indicate that 85.8% of hatchlings fledge. Commonest cause of nestling mortality is loss of parent. Nestlings hatched from eggs laid late in the season are subject to greater

mortality than are those from earlier eggs. Young breeders fledge relatively few nestlings in their first 2 yr of breeding (Fisher 1975a).

Of the pairs that have stayed together for 10–13 yr, 82–86% breed each year (Fisher 1976).

LIFE SPAN AND SURVIVORSHIP

Sixty-nine percent of females (started to breed at age 10 yr) and 65% of males (started breeding at age 9 yr) survived to age 17 yr (Fisher 1975a; determined by resighting of banded individuals). Five percent of fledglings banded in 1944 were recaptured, alive, at the age of 29 yr (Fisher 1975c). In 1972–1973 there were > 11 birds 40 yr of age or older (Fisher 1975c). Some bands could not be read, suggesting even older birds.

Fisher (1976) estimated the composition of his breeding colony at Midway to be: 54% prime reproductive birds aged 10–19 yr, 31% breeders 20 yr old or more, and 15% young inexperienced breeders. New breeders were recruited from the Midway colony itself.

MORTALITY AND DISEASE

Birds that start breeding early in life tend to die young (Fisher 1975a). Annual mortality rates are highest during the 3rd to 6th breeding years. In years 1, 2, and 7–9, mortality is half that during years 3–6.

Predation. Polynesian rats are the only predators in the breeding colonies in the Northwestern Hawaiian Islands, apart from man. The rats prey on adult birds at Kure Atoll, often killing them (Kepler 1967, Woodward 1972). In the main islands, dogs have killed Laysan Albatross and, on Oahu, the mongoose may be a threat. At sea, sharks and other large predatory fish probably take their toll of birds afloat.

Human/research impacts. Military activity killed many birds on Midway during World War II (Fisher and Baldwin 1946). Between 1954 and 1964, 54,000 birds were killed as a result of control measures to reduce risk of collisions with aircraft (Harrison et al. 1984) at Midway. In 1964–1965 communications antennas on Eastern I., Midway Atoll killed more than 3,000 adults that collided with them. Antennas were demolished in 1967 (Fisher 1970). Tall introduced *Casuarina equisetifolia* trees constitute a hazard to flying albatross at Midway Atoll, although providing protection to the nest and nestling.

Lights attract birds on Midway, resulting in night blindness and collisions with surrounding objects (Harrison et al. 1984). Collisions between aircraft and birds still occur at Midway. Small numbers of birds and eggs are taken, under permit, for scientific research.

At sea, the birds are caught on fish hooks and in Japanese salmon and squid gillnet fisheries (Robbins and Rice 1974, King et al. 1979, DeGange and Newby 1980, King 1984, Jones and DeGange 1988, McDermond and Morgan 1993). Estimated loss to driftnets in 1990 was 17,548 birds (McDermond and Morgan 1993), representing 0.7% of the total population.

Diseases and body parasites. The major cause of nestling mortality at Midway in 1987 was dehydration (accounting for 34%–51% of dead carcasses examined), followed by lead poisoning from paint (individuals pick up paint chips near the nest), leading to the condition of droop-wing and vehicular trauma (Sileo et al. 1990); starvation and trombidiosis were other causes. Non-fatal nocardiosis, parasite dermatitis, and avian pox also occur (Sileo and Sievert 1988). Latter is a viral disease, transmitted by introduced mosquitos (*Culex quinquefasciatus*); it causes facial lesions and may be fatal. Dehydration may be related to plastic ingestion—the plastics limit food, and hence water, intake. Introduced Beggartick (*Bidens alba*) is a preferred habitat for mosquitoes on Midway; birds nesting in this vegetation have a high incidence of avian pox (Fefer et al. 1984). A new species of chigger was described from a Laysan nestling (Goff et al. 1989).

RANGE

Initial dispersal from natal site. Initial dispersal is from the nest site to the beaches (Rice and Kenyon 1962b), followed by movement towards the reef and open ocean (Fisher 1967).

Fidelity to breeding site and winter home range. No birds banded as nestlings known to return to nest at their exact hatching site (Rice and Kenyon 1962b). For 3 or 4 yr prior to breeding, however, juveniles attempt to establish themselves and to nest near their natal site (Fisher 1976). Males breed, on average, 18.3 m from their natal nesting site, females 25 m (Fisher 1971b). Having nested once, they return to the same area, and often the same nest, year after year, even after landmarks in the colony have been destroyed (Rice 1959, Fisher 1971b). Nest-site tenacity is strong; experimental moving of nests > 1 meter results in rejection of the nest. Only 3 out of 1,078 fledglings in Fisher's plot at Midway nested outside the plot when they reached breeding age (Fisher 1976). Nevertheless, a few birds banded on one island have been captured on other islands as far apart as Kure and French Frigate Shoals, 1,158 km distant (Amerson 1971).

Home range. Includes territory in the immediate vicinity of the nest.

POPULATION STATUS

Numbers. Total population in the Hawaiian Is., with only small numbers elsewhere, is 2.5 million (Fefer et al. 1984, Harrison 1990). Of this total, 800,000 are breeders. Approximately 53% of the total breeding population selects Midway as their breeding colony (McDermond and Morgan 1993). Fisher (1966b) estimated that 39% of the birds at a breeding colony were incubating eggs, 39% would be the absent mates of those birds, and 22% were not incubating eggs. Nonbreeding birds reach peak percentage (51.3%) of birds at breeding colony (Kure) in Apr (Woodward 1972). Forty-five percent of nonbreeding birds at Midway are males (Rice 1959).

Trends. Population is expanding on Midway, Laysan I., and French Frigate Shoals in the Northwestern Hawaiian Islands (McDermond and Morgan 1993). In 1922 it was 5,000 on Midway; in 1945 the population was 110,000 (Fisher and Baldwin 1946, Fisher 1949); in 1992 close to 200,000 breeding pairs (Harrison 1990, McDermond and Morgan 1993). This may be due to diminished numbers of people on Midway but it may also represent recovery from the destruction of birds during past control measures (Harrison et al. 1984) and the stabilization of the sand dunes by imported top soil (Harrison pers. comm.). Population on nearby Kure Atoll is likely to increase also, following the closure of the U. S. Coast Guard station in 1992. Population is expanding into the main Hawaiian Is., islands off the Mexican coast, and the Bonin Is. (Hasegawa 1978, Kurata 1978, Byrd and Telfer 1980, Harrison et al. 1984).

POPULATION REGULATION

Needs study, especially in relation to food supply. Past populations were reduced by human predation and by climatic conditions such as El Niño episodes which may, in turn, have limited food availability. Expansion of the species to new islands suggests that the availability of nesting sites may have been regulating the population. More extensive squid fisheries may be a factor in the future (Harrison 1990).

CONSERVATION AND MANAGEMENT

EFFECTS OF HUMAN ACTIVITY

Japanese feather hunters decimated colonies at Midway, Laysan, and Lisianski at the turn of the century (see Distribution: historical changes). Former colonies at Volcano (Iwo), Wake, and Marcus islands have never recovered. Later, introduced rabbits so reduced vegetation on Laysan and Lisianski that nesting habitat was

harmed. Between 1958 and 1964, 2.4%–4.4% of aircraft landings and take-offs at Midway killed albatross (300–400 strikes/yr; Fisher 1966a, Robbins 1966). Collisions with antennas killed more than 3,000 albatross in 1964–1965 (Fisher 1970). Tens of thousands were removed in order to reduce the number of collisions. Eggs continue to be collected, and birds removed, from the vicinity of airfields. Not all human activity has been harmful: introduction of soil and grass to Sand I., Midway has greatly increased habitat for albatross.

Pesticides and other contaminants. Visceral fat contained appreciable amounts of phenyl-trichloroethane (DDT), 1, 1-bis-4-chloro-phebyl [2, 2-dichloro ethylene (DDE)], polychloro-biphenyl (PCB), and measurable amounts of dichlorodiphenyl dichloroethane (DDD), dieldrin, and mercury in 1969 (Fisher 1973); no known impact on reproduction. Oiled birds are seen repeatedly (Fefer et al. 1984, Harrison et al. 1984). Species rated moderately vulnerable to oil pollution (King and Sanger 1979).

MANAGEMENT

Birds colonizing Kilauea Point on Kauai in the main Hawaiian Is. have been protected from dogs (Byrd and Telfer 1980, Moriarty et al. 1986) and people by fencing. Birds have established a breeding colony there and they are carefully guarded by wildlife personnel. At Kure Atoll and Midway in the Northwestern Hawaiian Is., and at Barking Sands (Kauai), Dillingham Airfield (Oahu), and the Kaneohe Marine Corps Air Station (Oahu) in the main islands, birds have been discouraged from nesting in order to ensure aircraft safety.

APPEARANCE

MOLTS AND PLUMAGES

The following descriptions based on Palmer 1962, Rice and Kenyon 1962b, Dement'ev et al. 1968, Langston and Rohwer unpubl. ms.

Hatchlings. Born in late Jan or early Feb with first down (neoptile) feathers that have gray bases with white tips (more extensive than in Black-footed Albatross, giving a salt and pepper appearance).

Within a day or so after hatching, a second down (mesoptile) that is similar in appearance to the first down begins to replace first down (Post-natal I molt). Much bleaching from the sun may occur.

Albinism has been reported in nestlings (Fisher 1972), the bird having a mottled plumage. The

plumage aberrations occur mainly in the mantle and dorsum of the wings (Fisher 1972).

Juvenal plumage. Complete molt at 1 to 6 or 7 mo of age (Mar–Jul or Aug). Nearly identical to Definitive Basic plumage except for some gray feathers on upper thighs in some birds. Retained until the end of the next breeding season. Eleven primaries (number 11 is small and vestigial), 37 secondaries, 12 rectrices.

Basic I plumage. Prebasic I molt occurs at 16–21 mo of age (mid-Jun through early Oct on nonbreeding areas in North Pacific Ocean). Replaces all body plumage and outer 3 or, more rarely, 4 or 5 primaries in descendant (inner to outer) order (average 3.6 primaries). Also replaces an average of 7 secondaries in complex sequence. Timing of rectrix molt unknown. No known differences in color from Definitive Basic plumage.

Definitive Basic plumage. Definitive Prebasic molt occurs from age 34 months on (late Jun through mid-Oct on nonbreeding areas in North Pacific Ocean). Replaces all body plumage. Primaries 1–5 and 6–10 are molted as separate units and are under autonomous control. P1–P5 undergo "wraparound" molt (see below). P6–P10 are replaced in descendant sequence. All birds replace P8–P10 every year. At least 50% of birds also replace P7 or P6 and P7 (Langston and Rohwer unpubl. ms.).

Molt may begin at P6, P7, or P8, but always progresses through P10. The number of primaries replaced and the node at which molt begins in one year have no effect on the number of primaries replaced and the node at which molt begins the following year. All birds that do not replace all 5 primaries (P1–P5) will begin replacement of P1–P5 in their subsequent Prebasic molt with the most distal primary that was not replaced in the previous molt cycle, (e.g., if P5 and P4 are replaced in one molt cycle, then molt will begin with P3, not P5, in the next molt cycle). P5 will not be replaced a second time until all 5 inner primaries have been replaced once, thus the term "wraparound" molt (Langston and Rohwer unpubl. ms.).

P1 is sometimes replaced with the secondaries, rather than as part of the P1–P5 unit. Twenty percent of birds replace all primaries. Overall, birds replace an average of 6 primaries each year. The more primaries a bird replaces, the earlier it begins molt. An average of 11 secondaries are also replaced in complex sequence (Langston and Rohwer unpubl. ms.). Timing of rectrix molt is unknown.

Sexes similar in plumage. Head (except for blackish preocular patch), neck, underparts, and rump white. Head and neck sometimes tinged yellow. Tail blackish gray. Upper surface of wings

and back blackish gray becoming brownish by wear and bleaching. Underside white, sometimes tinged yellow and salmon. Eyes recessed beneath the supra-orbital ridges which may serve as eye shades. Dark feathers around the eye may also reduce light scatter into the eye (Warham 1990).

Hybrids. Hybrids (with Black-footed Albatross) are pearl gray, darker on the back (Fisher 1972).

BARE PARTS

Bill. Salmon-colored with gray tip. Tip of upper mandible turned down. Nostrils a separate tube on each side of the beak.

Iris. Brown.

Legs and feet. Flesh-colored. Toes fully webbed. Hybrids have darker bills, legs, and feet than the Laysan (Fisher 1972). Outermost layer of beak shed annually (Palmer 1962).

MEASUREMENTS

Linear. Overall length, bill length, neck thickness, and head width are greater in males than females (Frings and Frings 1961, Warham 1990, Appendix).

Mass. Body mass is higher in males than females (Appendix). Nonbreeders, as well as breeders, lose body mass during the breeding season (Fisher 1967).

ACKNOWLEDGMENTS

I am most grateful to my wife, Christina, for translating my illegible hand-writing into typescript and to Jane E. Inouye and Jean T. Komori for putting typescript onto disk. Paul R. Sievert and D. Ken McDermond kindly permitted access to their unpublished manuscripts. The Hamilton Library at the University of Hawaii kindly provided a room for my labors and every journal that I needed. The University of Hawaii permitted a short sabbatical which ensured that I had the time for this endeavor. An early draft of this account benefited from a reading by C. S. Harrison. Cover photo © P. La Tourrette/VIREO.

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Appendix. Mass (g) and linear dimensions (mm) of Laysan Albatross.

MASS ¹	MALE	FEMALE
ADULTS		
On arrival at the breeding colony	3310 ± 295 (50)	2990 ± 306 (20)
Start of incubation	3240 ± 232 (31)	2580 ± 329 (29)
End of incubation	3000 ± 216 (15)	2720 ± 193 (9)
End of period of intensive care of nestlings	2490 ± 211 (20)	2210 ± 217 (20)
End of breeding season	2880 ± 281 (19)	2660 ± 248 (21)
JUVENILES ²		
January	2730 ± 269 (11)	2510 ± 315 (19)
May	2400 ± 151 (19)	2040 ± 160 (25)
LINEAR DIMENSIONS ³	MALE	FEMALE
Head width	59.3 ⁴ ± 0.13 (129)	56.4 ⁴ ± 0.13 (112)
Bill length	172 ⁴ ± 0.31 (172)	101.4 ⁴ ± 15 (137)
Wing length	491.5 ⁵ (4)	495 ⁵ (1)
Tail length	142.5 ⁵ (4)	146 ⁵ (1)
Culmen length	107.1 ⁵ (4)	102 ⁵ (1)
Upper mandible	117.5 ⁵ ± 2.45 (18)	109.6 ⁵ ± 3.91 (68)
Depth	26.7 ⁵ (4)	27.1 ⁵ (1)
Width	29.8 ⁵ (4)	31.5 ⁵ (1)
Tarsus	82.8 ⁵ (4)	82 ⁵ (1)
Middle toe and claw	113.2 ⁵ (4)	112 ⁵ (1)
¹ Adults and juveniles at Midway Atoll. Mean ± standard deviation; number of birds in parentheses. Data from Fisher (1967). ² More than one year of age but not yet breeding. ³ Means ± SD. Number of birds in parentheses. ⁴ Frings and Frings 1961. ⁵ Loomis 1918. ⁶ Robbins 1966.		

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The Birds of North America is supported by charitable and governmental organizations including: The Office of Migratory Bird Management (USFWS), National Fish and Wildlife Foundation, The McLean Contributionship, The Geraldine R. Dodge Foundation, The Richardson Foundation, and the American Birding Association. Benefactors of this program include Wallace C. Dayton and Joseph and Helen Taylor.

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RECOMMENDED CITATION

Whitrow, G. Causey. 1993. Laysan Albatross (*Diomedea immutabilis*). In *The Birds of North America*, No. 66 (A. Poole and F. Gill, Eds.). Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.

