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DEMOGRAPHY AND NATURAL HISTORY OF LAYSAN ALBATROSS ON OAHU, HAWAII

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ABSTRACT.—Laysan Albatross (*Phoebastria immutabilis*) began re-colonizing sites across the Pacific in the 1970s after severe population declines, and fledged the first chick on the island of Oahu in 1992. We report the status of Laysan Albatross populations at Kaena Point and Kuaokala on the island of Oahu, Hawaii and provide new demographic data for this species. Colonies on Oahu were monitored weekly from 2004 to 2008; all individuals were censused, banded, and genetically identified to gender. There was a population of 365 adults on Oahu in 2008 of which 47% were active breeders. The breeding population increased 27% annually since 1991. The high rate of increase was due primarily to immigration with some local recruitment. Recaptures indicate that seven birds were from French Frigate Shoals, one was from Midway Atoll, and 52 were from Oahu and returning to breed; all other adults were of unknown origin. Hatching rate (62%), fledging rate (78%), and overall reproductive success (48%) were comparable to other colonies despite occasional predation. The rate of adult dispersal was high with up to 10% of birds observed each day on Oahu visiting from Kauai. Adults occasionally changed breeding colonies between seasons, and even visited other islands while actively breeding on Oahu. While small, these colonies are at higher elevations and may serve as refugia in the event of sea level rise and, thus, should continue to be conservation priorities. *Received 10 November 2008. Accepted 14 April 2009.*

The Laysan Albatross (*Phoebastria immutabilis*) has a broad distribution spanning tropical, subtropical, and subarctic zones (8° to 59° N) of the Pacific Ocean from the west coast of North America to Japan (Whittow 1993, Hyrenbach et al. 2002, Shaffer et al. 2005). Their pelagic habitat includes most of the North Pacific Ocean, but they have historically bred on a limited number of remote subtropical islands (Whittow 1993, Tickell 2000). Laysan Albatross began colonizing islands from Japan to Mexico in the 1970s, despite their reportedly high natal philopatry. Some sites were re-colonizations of islands where the species had been extirpated, such as Mukojima, Japan (Kurata 1978) and Wake Island in the Western Pacific (Rauzon et al. 2008), and Kauai in the main Hawaiian Islands (Zeillemaker and Ralph 1977, Tickell 2000). In addition to re-colonization of historical nesting sites, Laysan Albatross also recently expanded their range to several more islands, including Lehua Islet in the main Hawaiian Islands (VanderWerf et al. 2007), and into the Eastern Pacific on Isla Guadalupe, Clarion, and San Benedicto in Mexico (Gallo-Reynoso and Figueroa-Carranza 1996, Pitman et al. 2004).

Fossil evidence indicates that seabirds were not only present, but abundant in the main Hawaiian Islands before arrival of humans (Olson and James 1982, Moniz-Nakamura 1999, Burney et al. 2001). Seabird populations in the Hawaiian Islands severely declined following the arrival of Polynesians 1,500–1,900 years ago and subsequent arrival of Europeans over 200 years ago (Olson and James 1982, Harrison 1993, Moniz-Nakamura 1999). Laysan Albatross populations across the Pacific also severely declined during the early twentieth century as a result of human consumption, feather collecting, egg collecting, predation from introduced mammals, and military activities (Whittow 1993, Tickell 2000, Rauzon 2001). As a result, Laysan Albatross and many other breeding seabirds disappeared entirely from the eight main Hawaiian Islands (Olson and James 1982, Moniz-Nakamura 1999). Today, Laysan Albatross breed almost exclusively in the Northwestern Hawaiian Islands (NWHI; 97% of >600,000 pairs), which are largely free of

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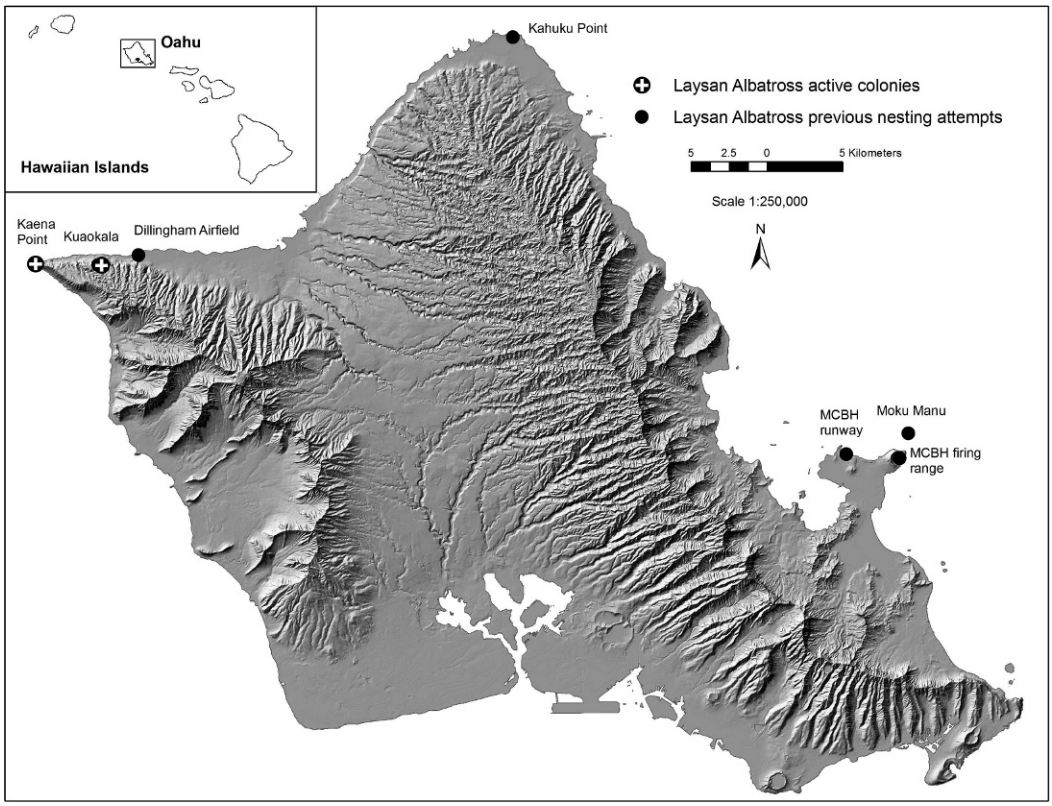

FIG. 1. Study sites and other locations on Oahu, Hawaii where Laysan Albatross have attempted to nest.

mammalian predators (Tickell 2000, Naughton et al. 2007).

Laysan Albatross are listed as vulnerable by the International Union for the Conservation of Nature (IUCN 2007) due to population fluctuations and high rates of at-sea mortality from bycatch in North Pacific fisheries (Gilman and Freifeld 2002). Understanding the status of each breeding population of Laysan Albatross has become a priority for developing conservation actions because this species is vulnerable and nests in few locations (Naughton et al. 2007). Laysan Albatross colonies on Oahu, Kauai, and Lehua in the Hawaiian Islands are currently small, but growing. Populations on these high islands may become increasingly important because they will be better able to withstand projected global climate changes and associated rises in sea level (Baker et al. 2006). Our objectives are to: (1) report the status of the Laysan Albatross population on Oahu, including a brief history of the species' occurrence, and (2) provide new demographic data for this species.

METHODS

Study Sites.—Detailed demographic monitoring of Laysan Albatross has occurred at two locations on Oahu in recent years, Kaena Point Natural Area Reserve (Kaena Point NAR), and Kuaokala Game Management Area (Kuaokala GMA) (Fig. 1).

Kaena Point NAR (21° 58′ N, 158° 27′ W) is on the westernmost tip of Oahu and protects 12 ha of arid coastal habitat ranging in elevation from sea level to 25 m. Mammalian predators, such as cats (*Felis catus*), dogs (*Canis lupus familiaris*), Indian mongoose (*Herpestes javanicus*), and black rats (*Rattus rattus*) are controlled by the U.S. Department of Agriculture (USDA), Wildlife Services through a combination of live trapping, shooting, and poison bait stations; however, these predators still survive at low densities. Two native plant communities are present, a mixed coastal dry shrubland dominated by naupaka (*Scaevola taccada*) and naio (*Myoporum sandwicens*), and a coastal dry mixed shrub and grassland dominated

by ilima (*Sida fallax*). Several introduced plants are also common, including koa haole (*Leucaena leucocephala*), kiawe (*Prosopis pallida*), and Guinea grass (*Panicum maximum*), although efforts are underway to remove these species. Laysan Albatross use all of these habitat types at Kaena Point NAR, including non-native vegetation.

Kuaokala GMA is ~6 km east of Kaena Point NAR at 350 m elevation in the northern Waianae Mountains (21° 56′ N, 158° 23′ W) and is the highest Laysan Albatross colony in the world. The habitat is dominated by introduced ironwood (*Casuarina equisetifolia*), strawberry guava (*Psidium cattleianum*), and introduced grasses. The area where most albatross nest is fenced, and is part of a pig and game bird hunting area within the Mokuleia Forest Reserve. Most nesting occurs under ironwood trees, where the needles from the trees are used to build nest cups.

Monitoring Techniques.—All chicks at Kaena Point NAR and Kuaokala GMA were censused and banded starting in 1992. Regular monitoring of adults and chicks at both colonies began in 2004 for the duration of the breeding season (Nov–Jul), and all birds encountered were captured by hand and banded with a federal metal band with a unique serial number. Monitoring consisted of a weekly census of all birds present in the colony at Kaena Point NAR, and approximately monthly at Kuaoakal GMA. Starting in 2006, each bird was also given a field-readable purple plastic band numbered in white from O001–O999. A small (400 uL) blood sample was collected from the tarsal vein of each bird for use in identifying gender and other genetic analyses. All individuals were classified to gender following protocols outlined in Fridolfsson and Ellegren (1999) and Young et al. (2008). Previously banded birds were reported to the Bird Banding Laboratory which provided information on the origin and, in some cases, age of each bird.

Nesting attempts were monitored from egg-laying through chick fledging. Each time an adult was encountered, its location, status (incubating, brooding, or walking), and association with any other adult or chick were recorded. Chicks were observed approximately weekly from hatching (Feb) until fledging (Jul) each year. Nest number, parent information, hatching date, disease status, and date of either fledging or death were recorded for all chicks. Chicks that survived to fledging age were banded with both a federal metal band and a field-readable plastic band.

Analyses.—We estimated the number of Laysan Albatross that have been recorded on Oahu since the 1970s by compiling banding records and observations from the published literature, federal banding records, and discussions with biologists and birders. Individuals were included only if a band number could be obtained to ensure the actual number of individuals, and not just observations, was reported.

Size of the non-breeding population is difficult to estimate in seabirds (Citta et al. 2007), but we attempted to estimate the total current Laysan Albatross population on Oahu by summing the numbers of birds that have bred at least once in the past 3 years (to account for birds that skipped up to 2 years), non-breeders that have visited the island at least twice in the past 5 years (since some non-breeders do not visit every year), and chicks hatched on the island that returned and visited the island at least twice in the past 4 years. These time periods were chosen based on attendance patterns of birds in each category and the encounter probability of each category.

We calculated the average rate of increase in the breeding population from 1992 (year the first chick fledged) to 2008 using the formula: $k = (n_t/n_0)^{-t}$ where k is the rate of increase, n is the number of nesting pairs, and t is time in years.

RESULTS

Population History.—Laysan Albatross have attempted to breed at six locations on Oahu since 1979: Kaena Point NAR, Kuaokala GMA, Kahuku Point, and Dillingham Airfield on Oahu's northern coast, and Kaneohe Marine Corps Base (MCBH) and Moku Manu on the eastern side of Oahu (Fig. 1). The two sites on Oahu where Laysan Albatross have successfully established and maintained colonies are Kaena Point NAR and Kuaokala GMA. The Kahuku Point colony failed to fledge any chicks due to predation by dogs and, in 1996 the remaining adults abandoned breeding there altogether but still regularly visit the site (Mike Ord, Pete Donaldson, Mike Silbernagle, pers. comm.; LCY and EAV, pers. obs.). Laysan Albatross attempted to nest at Dillingham Airfield during the late 1980s and 1990s, but due to the strike hazard they posed to aircraft, eggs were removed to discourage nesting (Mark Ono, pers. comm.); adults still regularly

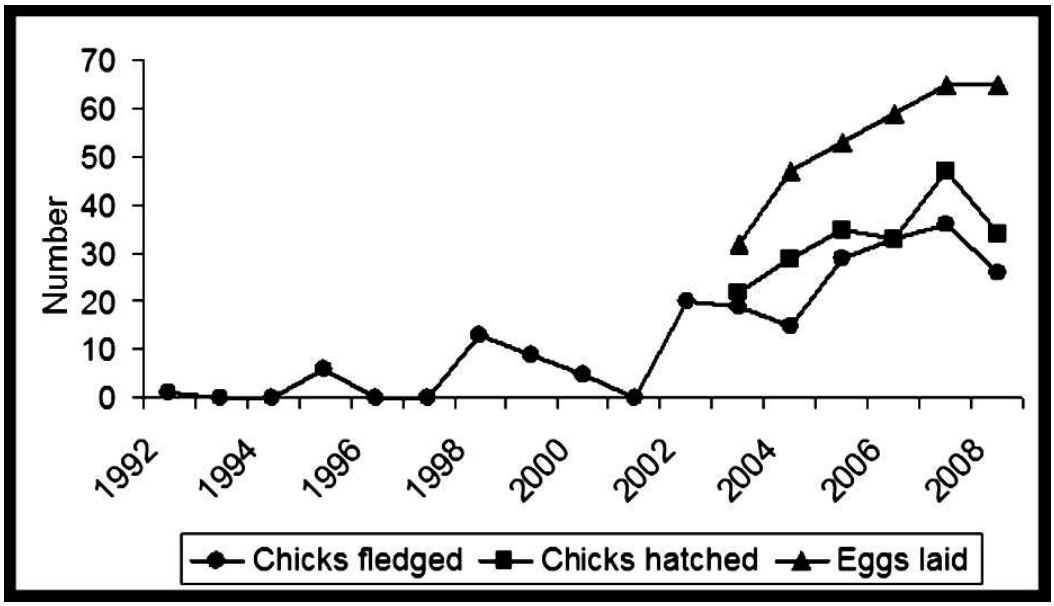

FIG. 2. Number of chicks fledged each year from Laysan Albatross colonies on Oahu, Hawaii since 1992 and numbers of eggs laid and chicks hatched from 2004 to 2008.

visit the site. Laysan Albatross still attempt to nest each year near an active runway at MCBH and, at times, in an active firing range (Diane Drigot, pers. comm.). Eggs are removed at this site to discourage nesting and reduce the chance of aircraft strikes. All adults encountered at MCBH since 1985 have been banded by USDA, Wildlife Services personnel and removed from the site; some have been released at Kaena Point NAR.

Population Size and Origin of Laysan Albatross on Oahu.—The annual growth rate of the Laysan Albatross breeding population on Oahu was 27% from 1992 to 2008. This growth was primarily a result of immigration from other colonies, but there was some local recruitment. The number of chicks fledged also increased over the same time period (Fig. 2). The total population size on Oahu in 2008 was ~365 adults of which 163 (47%) were breeders. Kaena Point NAR is the larger of the two colonies (28–50 nests from 2004 to 2008) and has two to three times the population of Kuaokala GMA (15–23 nests from 2004 to 2008). The sex ratio of adults in the Oahu population was female-biased (59% female), although, the sex ratio of chicks at fledging was 49% female.

A total of 891 Laysan Albatross has been recorded on Oahu from 1979 to 2008. Of these, 264 (30%) were chicks hatched on Oahu, 193 (22%) were adults that bred at least once since 2003, and 434 (48%) were non-breeding adults. Most adults on Oahu did not have bands when first observed (78%, $n = 494/627$) and are of unknown origin. Of birds banded as chicks and, thus, of known origin ($n = 59/627$; 9%), seven were from French Frigate Shoals, one was from Midway Atoll, and 52 were Oahu individuals recruiting to their natal colony. Two chicks hatched on Oahu were observed as adults on Kauai (Brenda Zaun, unpubl. data) and have not returned to their natal colony. Birds banded elsewhere as adults were exclusively from Kauai ($n = 76/365$ adults) and comprised 21% of the current adult population on Oahu. This observation, coupled with chicks from Oahu recruiting to Kauai, provides evidence of both natal and adult dispersal in this species.

Reproductive Success and Behavior.—The overall nest success rate on Oahu from 2004 to 2008 was 48% (Fig. 3). The hatching rate of all eggs laid was 62%, and the fledging rate of all chicks hatched was 78%. The number of nesting attempts steadily increased despite variation in hatching and fledging success as a result of predation (Fig. 3). Breeding phenology closely parallels other Laysan Albatross colonies with the first birds returning to the colony during 6–11 November, egg laying from 21 November to 16 December, chicks hatching from 25 January to 21 February, and chick fledging occurring primarily in July.

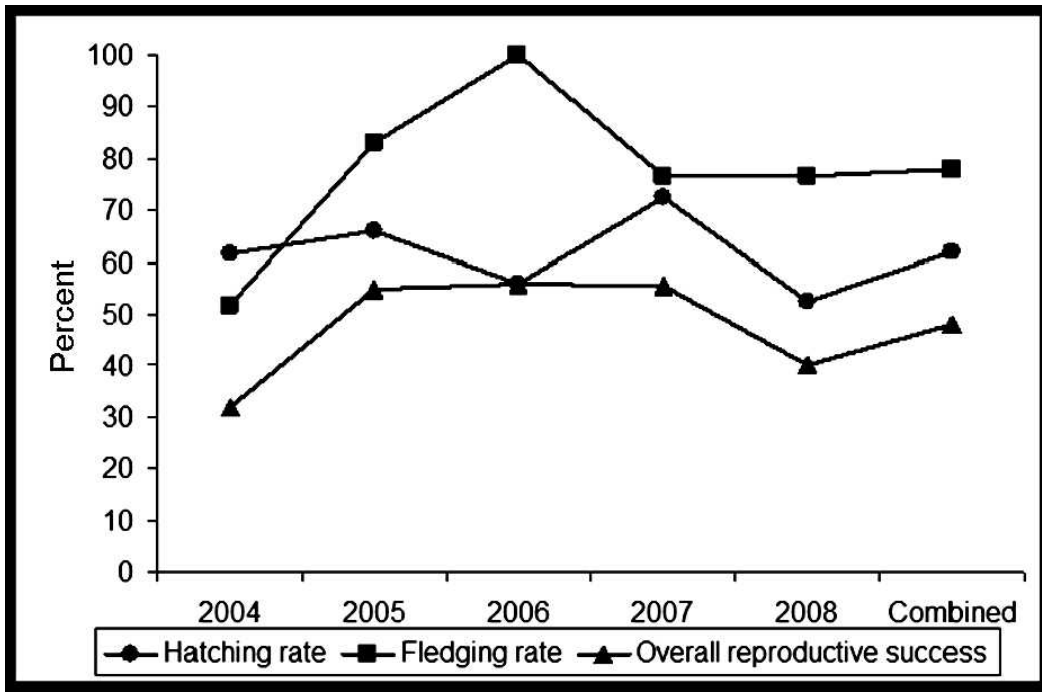

FIG. 3. Rates of hatching (% of eggs laid that hatch), fledging (% of chicks hatched that fledge), and reproductive success (% of eggs laid that result in fledged chicks) for Laysan Albatross on Oahu, Hawaii.

The rate of mate change in Laysan Albatross on Oahu was 14% (9/66), based on pairs in which the mate was known for at least 3 years. A mate change was defined as two birds pairing for at least 2 years then at least one of the birds pairing with a different bird when its previous mate was known to be alive. Eight of nine pairs that changed mates were reproductively successful in their breeding attempt preceding the mate change on Oahu. The chance of changing mates was related to one partner taking a year off and not returning to the colony during that year to reaffirm the pair bond. Five of nine mate changes occurred when one mate returned to the colony and the other did not. Five of the nine birds found a new mate and nested the same season their partner did not return, and four skipped 1 year before breeding with a new mate. In one case a bird returned to its original mate the following year despite breeding with a different bird while its mate was absent.

DISCUSSION

In 1947 a single Laysan Albatross chick was recorded at Moku Manu Islet off Oahu (Fisher 1948) and an abandoned egg was found there the following year (Richardson and Fisher 1950), but it wasn't until 1978 that adults began regularly appearing at several locations around the island (Pyle 1978, 1986; Pratt 1988). Breeding attempts that began in 1979 at Kahuku Point were not successful due to predation and crushing of nests by off-road vehicles (Eilerts 1987). Laysan Albatross colonies on Oahu have grown rapidly since the first chick fledged from Kaena Point NAR in 1992. This success has been made possible by protection and active management of nesting areas, particularly exclusion of off-road vehicles beginning in 1991 and control of alien predators beginning in 1995. These actions have allowed immigrating birds to flourish and the colony to grow despite the continual threat of predation, introduced diseases, and interference from humans (VanderWerf et al. 2005, Young and VanderWerf 2008).

A social attraction project using decoys and sound recordings began in 1993 at Kaohikaipu Island off Oahu's eastern shore in an attempt to attract Laysan Albatross to nest on predator-free (and people-free) islets (Borzik et al. 1995). There were no breeding attempts and the project was discontinued, despite visits by adults during the

project with the sound system ceasing to function in 1995 (Kress et al. 1999) and removal of the decoys in March 2000. Several hundred Laysan Albatross were banded on Oahu during the social attraction project and the project's failure was not due to lack of birds but, perhaps, because of some unsuitable characteristic of Kaohikaipu.

The rapid growth of these colonies cannot be attributed to successful local reproduction alone, because the total number of chicks fledged from 1992 to 2008 was much less than the number of recruits arriving at the colonies. Some birds hatched on Oahu have returned to their natal area and begun breeding, but a much larger proportion of new breeders originated from other islands, and the female-biased sex ratio in the colony is a byproduct of female-biased immigration (Young et al. 2008). Six of seven band recaptures from birds hatched in the NWHI and now present on Oahu were from Whale-skate Island in French Frigate Shoals, which disappeared in 1997 after decades of erosion, displacing thousands of birds (Beth Flint, pers. comm.). It is possible that colonization events were initiated across the Pacific as the result of displacement of albatross from Whale-Skate Island, and these new colonies now attract dispersing birds from other colonies in the NWHI as a result of social facilitation. Three of six birds from Whale-skate now breeding on Oahu were banded as chicks within 1 day of each other in 1992, indicating they may have been traveling as a cohort. Traveling as a cohort has not been documented in this species, but is worth investigating as this may provide insights into colonization mechanisms in this, and other, colonial seabird species.

Recent counts of Laysan Albatross at Midway, Laysan, and Tern islands in the NWHI, which account for ~93% of the global population, have also indicated stable or growing numbers of breeding birds (Beth Flint, pers. comm.); the increase on Oahu and at other new colonies may be related to this growth. Juvenile dispersal by Wandering Albatross (*Diomedea exulans*) is density dependent, leading to higher juvenile dispersal when local population density is high (Inchausti and Weimerskirch 2002). Increases at new colonies may be driven by juveniles dispersing from high density nesting colonies in the NWHI if a similar mechanism is functioning in Laysan Albatross. Previous studies of Laysan Albatross have reported high natal philopatry, but these early studies (Fisher and Fisher 1969) could have missed immigration or emigration because they were done using a plot design within large colonies, and did not track the fate of individuals that left the plot. The exact cause of the range expansion of Laysan Albatross is unknown, but a combination of factors are likely responsible for supplying recruits to new colonies.

Adult dispersal was also documented with non-breeding adults regularly visiting other colonies, at times several times daily through the duration of the breeding season; breeding adults occasionally switched breeding colonies between years. Up to 10% of the birds observed on Oahu any given day were non-breeding adults visiting from Kauai. Moreover, when both colonies on Oahu were monitored on the same day, 1–2 individuals were often observed at both sites. The same phenomenon has been observed on Kauai, where Oahu non-breeding birds are regularly seen visiting (Brenda Zaun, pers. comm.). One adult banded on Oahu at 1000 hrs HST on 14 January 2006 was observed at 1600 hrs HST the same day at Kilauea Point on Kauai, 137 km away (Brenda Zaun, pers. comm.). Another individual from Kauai was observed on Oahu, and then at Lehua Islet 73 km west of Kauai 8 days later. Most birds moving among colonies are non-breeders and are likely to be young individuals searching for a breeding site, but some are active breeders or birds taking a year off, including one 19-year old adult from French Frigate Shoals observed at Kaena Point NAR in 2008. Each year on Oahu, 1–2 breeding pairs switch from breeding at Kuaokala GMA to breeding at Kaena Point NAR and vice versa. This could be interpreted as low site fidelity, but it is possible the birds functionally treat these sites as a single colony since they are within sight of one another. These observations support the hypothesis that Laysan Albatross are aware of nearby colonies and regularly visit them to gather information and prospect for suitable breeding sites and/or mates as has been reported for other seabirds (Danchin et al. 1998).

Observations of the breeding behavior of Laysan Albatross on Oahu have also provided new insights into this species' natural history. The high rates of mate change, super-normal clutches, and same-sex pairing (Young et al. 2008) observed on Oahu are all previously unreported for this putatively socially-monogamous, single-egg clutch species. The 14% rate of mate changing is higher than the 9% previously reported for this species (Fisher 1971, 1976).

Mate change in previous studies was reported to be associated with breeding failure (Fisher 1971, Bried et al. 2003), but this was not true on Oahu where the chance of a mate change appeared to be related to one member of a pair taking a year off when the other returned to the colony.

There were several observations of successful single-parent nests in this colony, which has not been reported previously in this species. In 2006, when a female was killed as bycatch by a Taiwanese long-lining vessel, the male partner successfully fledged the week-old chick without assistance from his mate. Additionally, in 2008, one male maintained two separate nests with two different females and successfully fledged both chicks (which accounts for the odd number of 163 breeding birds). These observations indicate that a single parent can fledge a chick, although in both cases the chicks appeared to be underweight and were the last to fledge from the colony. These behaviors have also been observed on Kauai (Brenda Zaun, pers. comm.), indicating they are not unique to Oahu, but typical of this species' natural history.

Regular monitoring that included census of all individuals was possible due to the small size and accessibility of the Laysan Albatross colonies on Oahu, and has provided natural history information and observations on this species that are not possible in larger, less accessible colonies (Young and VanderWerf 2008, Young et al. 2008). Estimation of reproductive and population parameters, such as the proportion of breeders and nonbreeders, is more feasible for the small population on Oahu than in larger colonies and can serve as a guideline to complement the monitoring occurring at other colonies.

The return of nesting Laysan Albatross and other seabirds to the main Hawaiian Islands is the result of years of predator control and habitat restoration projects initiated by several state and federal agencies. Black-footed Albatross (*Phoebastria nigripes*) and 11 other species of seabirds have been observed at Kaena Point NAR and, with continued habitat restoration and mammalian predator control, some of these species may recolonize the main Hawaiian Islands. A predator-proof fence that would exclude all mammalian predators is now in the planning stages for Kaena Point NAR, which will result in improved protection for nesting Laysan Albatross, thousands of nesting Wedge-tailed Shearwaters (*Puffinus pacificus*), and 11 federally endangered plant species (Hawaii Department of Land and Natural Resources 2007). The Laysan Albatross colonies at Kaena Point NAR and Kuaokala GMA are small, but may be critically important for the long-term survival of the species because they are among the few high island nesting sites that may serve as refugia should projected rises in sea level inundate primary nesting sites in the Northwestern Hawaiian Islands (Baker et al. 2006). Conservation efforts should continue to focus on protecting these colonies.

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