



ESTIMATING SURVIVAL AND LIFE-STAGE TRANSITIONS IN THE LAYSAN ALBATROSS (*PHOEBASTRIA IMMUTABILIS*) USING MULTISTATE MARK–RECAPTURE MODELS

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ABSTRACT.—Accurate estimates of demographic rates are fundamental to understanding population dynamics and can provide insights into the ecology and conservation of a species. We used multistate mark–recapture models to estimate apparent annual survival, encounter probability, and life-stage transitions in Laysan Albatrosses (*Phoebastria immutabilis*) at Kaena Point, Hawaii, from 2003 to 2010. Four-state models of prebreeders, breeders, failed breeders, and skipped breeders overestimated survival by 1–3% and underestimated skipped breeding by 5–6%, but five-state models that included a state for unobserved skipped breeders performed better. Survival did not vary among years and was highest in prebreeders (mean \pm SE = 0.996 ± 0.010) and lower in successful breeders (0.932 ± 0.023) than in failed breeders (0.963 ± 0.018), suggesting a cost to reproduction. Survival was similar in males and females among prebreeders, breeders, and failed breeders, but survival of males was lower among skipped breeders. Encounter probability was related to monitoring effort; more frequent visits and use of field-readable auxiliary bands and remote cameras resulted in higher encounter rates. With sufficient effort, all skipped breeders were observed at the colony even though they did not breed. Recruitment averaged 24% in females and 21% in males and varied among years. Breeding frequency averaged 0.807 ± 0.028 and varied among years. Successful breeders were more likely than failed breeders to skip the next breeding season. Estimates of all demographic rates except recruitment were similar to estimates for Laysan Albatrosses from Midway in the 1960s despite differences in methodology. This information can help measure population dynamics, breeding population sizes, population trends, and efficacy of conservation actions. *Received 19 December 2010, accepted 16 June 2011.*

Key words: breeding frequency, encounter probability, Laysan Albatross, mark–recapture models, *Phoebastria immutabilis*, recruitment, survival.

Estimación de la Supervivencia y las Transiciones en los Estadios de Vida en *Phoebastria immutabilis* usando Modelos de Estado Múltiple de Marcado y Recaptura

RESUMEN.—Los estimados precisos de las tasas demográficas son fundamentales para entender las dinámicas poblacionales y pueden brindar información sobre la ecología y conservación de las especies. Usamos modelos de estado múltiple de marcado y recaptura para estimar la supervivencia anual aparente, la probabilidad de encuentro y las transiciones en los estadios de vida en *Phoebastria immutabilis* en Kaena Point, Hawái, desde 2003 a 2010. Los modelos de cuatro estadios de individuos (pre-reproductivos, reproductivos, reproductivos fallidos y que pasaron por alto la reproducción) sobreestimaron la supervivencia en un 1–3% y subestimaron a los individuos que pasaron por alto la reproducción en un 5–6%. Sin embargo, los modelos de cinco estadios que incluyeron un estadio de individuos no observados que pasaron por alto la reproducción tuvieron un mejor desempeño. La supervivencia no varió entre años y fue máxima en los individuos pre-reproductivos (media \pm EE = 0.996 ± 0.010) y menor en los individuos reproductivos exitosos (0.932 ± 0.023) que en los individuos reproductivos fallidos (0.963 ± 0.018), lo que sugiere un costo de la reproducción. La supervivencia fue similar en los machos y las hembras entre los individuos pre-reproductivos, reproductivos y reproductivos fallidos, pero la supervivencia de los machos fue menor entre los individuos que pasaron por alto la reproducción. La probabilidad de encuentro se relacionó con el esfuerzo de monitoreo; las visitas más frecuentes y el uso de anillos auxiliares legibles en el campo y de cámaras remotas dio como resultado tasas de encuentro más altas. Con esfuerzo suficiente, todos los individuos reproductivos que pasaron por alto la reproducción fueron observados en la colonia aunque no se reprodujeron. El reclutamiento promedió 24% en las hembras y 21% en los machos y varió entre años. La frecuencia de reproducción promedió 0.807 ± 0.028 y varió entre años. Los individuos reproductivos exitosos tuvieron una mayor probabilidad de pasar por alto la estación reproductiva siguiente que los individuos que pasaron por alto la reproducción en el año de estudio. Los estimados de todas las tasas demográficas excepto el reclutamiento fueron similares a los estimados para *Phoebastria immutabilis* de Midway en la década de 1960 a pesar de las diferencias metodológicas. Esta información puede ayudar a medir las dinámicas poblacionales, los tamaños poblacionales de individuos reproductivos, las tendencias poblacionales y la eficacia de las acciones de conservación.

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ACCURATE ESTIMATES OF demographic rates are fundamental to understanding population dynamics, and examining patterns of variation in parameters such as survival and recruitment can provide insights into the ecology and conservation of a species (Nur and Sydesman 1999, Véran et al. 2007, VanderWerf 2008). Life-history theory predicts a tradeoff between survival and reproduction, leading to a balance between current reproductive effort and residual reproductive value (Williams 1966, Stearns 1992). In long-lived species, individuals should be less likely to compromise their own survival by increasing reproductive effort, sometimes resulting in delayed recruitment and intermittent breeding (Curio 1983, Weimerskirch 1992, Jouventin and Dobson 2002). The balance between survival and reproduction may differ between the sexes and among age classes, and it can also be affected by environmental variation and predictability (Erikstad et al. 1998, Oro et al. 2010, Cubaynes et al. 2011).

Large seabirds like albatrosses (Diomedidae) are classic examples of long-lived species, being characterized by high adult survival, low fecundity, delayed recruitment, and intermittent breeding (Tickell 2000). These life-history traits and their colonial nesting habits and wide distributions at sea also make albatrosses vulnerable to a variety of anthropogenic threats. Albatrosses are one of the most imperiled groups of birds, with 17 of 22 species considered threatened under IUCN criteria and the remaining five species considered near-threatened (IUCN 2010). The threats include mortality of adults from fisheries bycatch (Tasker et al. 2000, Tuck et al. 2001, Véran et al. 2007, Finkelstein et al. 2008, Žydelis et al. 2009), predation by alien species at nesting colonies (Wanless et al. 2007, Jones et al. 2008), bioaccumulation of contaminants (Guruge et al. 2001, Finkelstein et al. 2006), and ingestion of plastic (Sievert and Sileo 1993, Young et al. 2009a).

Albatrosses and other colonial seabirds are well suited, in some respects, to mark-recapture studies and other demographic research because they are easy to capture and resight, have high site fidelity, and nest on the surface in dense aggregations (Weimerskirch et al. 1987), but other aspects of their life history can complicate mark-recapture analyses and lead to biased survival estimates (Kendall et al. 2009). In particular, albatrosses sometimes skip breeding seasons, and breeding frequency varies among and within albatross species, depending on several biological and environmental factors, such as body size and length of the nesting cycle, previous reproductive success, body condition, and foraging ecology and food availability (Fisher 1976, Weimerskirch 1992, Jouventin and Dobson 2002, Ryan et al. 2007). Breeding frequency is lowest in the largest species (*Diomedea* spp.), in which the nesting cycle is so long that all successful breeders must skip the next breeding season, and generally higher in smaller species such as Laysan Albatross (*Phoebastria immutabilis*) that can complete a nesting cycle each year but occasionally skip a season (Jouventin and Dobson 2002).

It has been assumed that most nonbreeding albatrosses do not visit the colony or do so only rarely, which would constitute temporary emigration and cause biased survival estimates using conventional mark-recapture models (Kendall et al. 1997, Schaub et al. 2004). Multistate mark-recapture models that allow individuals to transition among life-history states provide a means of accounting for temporary emigration through use of an unobservable state (Fujiwara and Caswell 2002, Kendall and Nichols 2002,

Schaub et al. 2004) and have been useful for modeling survival of skipped breeders (Cubaynes et al. 2011) and of successful breeders in species with biennial breeding (Converse et al. 2009).

Most information on the demography of the Laysan Albatross comes from the pioneering work of Harvey Fisher at Midway Atoll in the 1960s and 1970s (e.g., Fisher 1975a, b, 1976). Fisher's work provided a wealth of information about most aspects of the species' demography and addressed many issues that are still of interest today, but more recent data are needed to help understand the current status, dynamics, and threats to the species and in making informed management decisions for this and other species with similar life histories (Arata et al. 2009). For example, compensatory mitigation using eradication of predators from nesting islands has been proposed as an alternative to reduction of fishery bycatch, but meaningful evaluation and comparison of these methods is dependent on accurate estimates of survival, recruitment, and other parameters (Wilcox and Donlan 2007, Finkelstein et al. 2008, Žydelis et al. 2009). Population size is fundamental to assessing conservation status, and albatross breeding populations are often estimated using a correction factor for the proportion of birds that skip breeding each year, but small differences in this proportion can cause large differences in breeding population estimates, potentially obscuring population trends (Arata et al. 2009).

Here, we report on survival, encounter probability, and transition rates among life stages of Laysan Albatrosses at Kaena Point, Oahu. This site provides an excellent opportunity to investigate albatross demography because it is readily accessible and easily monitored, and because the small colony size makes it possible to census all individuals on each visit. Several previous studies have used multistate mark-recapture models to investigate survival and breeding frequency of albatrosses and other long-lived seabirds (Oro et al. 2010, Cubaynes et al. 2011), and use of unobservable states to represent skipped breeders is a valuable technique (Converse et al. 2009, Kendall et al. 2009). We compared performance of four-state models incorporating states for prebreeders, successful breeders, failed breeders, and observed skipped breeders with five-state models that employed an additional state for unobserved skippers. Division of skipped breeders into observed and unobserved states is a new approach that we believe can help advance estimation of demographic parameters in long-lived animals with variable breeding frequency and improve design of monitoring programs for such species.

METHODS

Study area and population.—Kaena Point Natural Area Reserve is located on the westernmost tip of Oahu (21.58°N, 158.27°W) and protects 24 ha of arid coastal habitat ranging in elevation from sea level to 30 m. The Laysan Albatross colony at Kaena Point is one of the most accessible albatross colonies in the world; it lies at the end of a 3.5-km dirt road an hour's drive from urban Honolulu and is open to the public. Laysan Albatrosses have bred at other locations on Oahu, including Kuaokala Game Management Area (Young et al. 2009b), which is located 4 km from Kaena Point, but the present study was focused exclusively on the Kaena Point colony because it has been monitored most intensively. The Kaena Point colony is relatively new and small, but it has grown steadily from the first

successful nest in 1992 to a maximum of 57 nests in 2010 (Young et al. 2009b, L. C. Young et al. unpubl. data). Adults arrive in November, eggs are laid in late November and early December, and young fledged in June–July. Alien mammalian predators were controlled during the present study, including feral cats (*Felis catus*), dogs (*Canis familiaris*), and small Indian Mongooses (*Herpestes auro-punctatus*), but were still present in reduced densities.

Data collection.—We monitored Laysan Albatrosses at Kaena Point from November to July during the 2003–2010 breeding seasons. Each breeding season spanned two calendar years, so we referred to breeding seasons by the year in which young fledged. All young hatched at Kaena Point have been marked with a federal leg band with a unique serial number, beginning with the first successful nest in 1992. In 2003, all breeding adults were checked for bands but no additional adults were banded. Monitoring effort increased after 2003, when we began visiting the colony more often and introducing additional monitoring techniques. In 2004 and 2005, we captured and banded all birds with a federal band, including breeders and nonbreeders. In 2006, we began marking all birds with a federal band and a field-readable colored plastic leg band to allow identification of birds at a distance. In 2010, we deployed four remote cameras with infrared motion-sensitive triggers in areas of the colony where nonbreeding birds congregated to augment resighting of color-band numbers.

We began each visit by identifying birds from a distance by their color bands using binoculars, then capturing any unbanded birds and checking the identity of birds sitting on nests. Because the colony is small and birds were readily visible in the open habitat, we often identified or captured every bird present. We collected a small (400 μ L) blood sample from the tarsal vein of each bird for genetic sexing and other genetic analyses. All individuals were sexed following protocols in Young et al. (2008) and Fridolfson and Ellegren (1999). Birds banded elsewhere were reported to the U.S. Geological Survey Bird Banding Laboratory, which provided information on the origin and age of each bird.

Data analysis.—We created an encounter history for each bird using the year of initial capture and recaptures and resightings in subsequent years. We encountered a total of 418 adult Laysan Albatrosses at Kaena Point from 2003 to 2010, of which 249 met criteria for inclusion in analyses of adult survival and life-stage transition. We included all birds of known sex that bred at Kaena Point at least once ($n = 157$) and nonbreeding birds of known sex that were encountered at Kaena Point at least twice ($n = 92$). Birds that hatched at Kaena Point were included once they returned to the colony after fledging, so this analysis did not include survival of juveniles during their first year. We excluded birds first encountered in 2010 because they were not yet informative ($n = 67$). We excluded birds encountered only once and considered them transients ($n = 85$), including birds banded on Oahu but of unknown origin and birds banded elsewhere (most often Kauai) and seen on Oahu only once. We also were forced to exclude 17 birds of unknown sex, from which a blood sample was either not collected or the PCR-based sexing technique was unsuccessful.

We used four-state and five-state models in Program MARK, version 6.1 (White and Burnham 1999, Cooch and White 2011), to generate maximum-likelihood estimates of apparent annual survival (ϕ), encounter probability (p), and transition probability (ψ) of Laysan Albatrosses among states representing different life stages.

Four-state models included four observable states: prebreeders (P), birds not known to have bred in any year, most of which were young birds from 2 to 6 or 7 years old; breeders (B), birds that bred successfully in a given year; failed breeders (F), birds that attempted to breed in a given year but failed; and skipped breeders (S), birds that had bred before but skipped breeding in a given year yet were observed at the colony. Five-state models employed an additional state representing unobserved skipped breeders (U), birds that had bred before but skipped breeding and were not observed in a given year but were observed in a subsequent year and, thus, were known to have survived. We grouped birds by sex, and each bird was classified into one of the states each year. Some life-stage transitions were not biologically possible and their probabilities were therefore fixed at zero. For example, breeders, failed breeders, and skipped breeders could not revert back to the prebreeder state, and prebreeders could not transition to skipped breeder. Our survival estimates represent apparent survival because the population sampled was open and the fate of birds was unknown. Although we visited the colony multiple times each season, we did not use robust-design models because the secondary sampling periods were not effectively closed due to variation in timing of visitation among different groups and ages of nonbreeders (Kendall et al. 1997). We used a time-specific parameter structure to model apparent survival and transition among states. Use of an age- and time-specific parameter structure would allow examination of parameter changes associated with maturation, but doing so would require excluding immigrants of unknown age, which would have resulted in a data set too small in some years. Moreover, Weimerskirch (1992) found that survival did not vary with age within life stages and that breeding frequency depended primarily on body condition rather than age. This study encompassed a period of 8 years (2003–2010), so there were seven annual intervals. Five birds were coded with a frequency of -1 because they were known to have been removed from the population during the study because of mortality from predation at the colony or from fishery bycatch at sea. Model notation follows Lebreton et al. (1992), in which subscripts indicate whether parameters differed among groups (e.g., ϕ_{sex}) or years (ϕ_{yr}) or were constant, indicated by a dot (ϕ).

For both four-state and five-state scenarios, we began with the simplest model in which all parameters were constant, then added parameters to examine patterns of biological interest, such as differences between the sexes and variation among years. The fit of models was compared with Akaike's information criterion corrected for small sample size (AIC_c). The model with the lowest AIC_c value was considered to have the best fit. Models with AIC_c values that differ (ΔAIC_c) by ≤ 2 are also generally considered to have a reasonable fit (Burnham and Anderson 2002); in this case, we considered models with ΔAIC_c up to 2.30 because several models had values slightly above and below 2.0, and there was a natural break above 2.30. Goodness-of-fit tests are difficult to perform on multistate models that include an unobservable state with fixed parameters using the methods available in MARK, such as the median \hat{c} method. Instead, we conducted a series of goodness-of-fit tests using the U-CARE program as prescribed by Choquet et al. (2005), which indicated that it was not necessary to apply an overdispersion factor, or \hat{c} .

As another measure of recruitment, we calculated the proportion of first-time breeders in the population each year from

2006 to 2010. We did not calculate this proportion in earlier years because some breeders were not banded in 2003, and those birds could have skipped breeding in 2004 and erroneously appeared as first-time breeders in 2005. Results are presented \pm SE.

RESULTS

Model performance.—The best-fitting models were similar in the four-state (Table 1, model 1) and five-state (Table 2, model 1) scenarios, and the best five-state model included additional parameters involving unobserved skippers that were not possible in the four-state model. Five-state models performed better and were less biased than four-state models in several ways. Five-state models correctly estimated encounter probability of breeders and failed breeders at 1.0 (Table 3), which we knew to be the true value because of our ability to census breeders at this site. By contrast, encounter probability of breeders was underestimated in four-state models because some unobserved skippers were erroneously counted as missed breeders. Survival of some groups was overestimated in four-state models by 1–3%, including male skippers, female breeders, and female failed breeders (Table 3). Four-state models that included only observed skippers underestimated the rate of skipped breeding. An accurate estimate of skipped breeding was obtained from five-state models by adding unobserved skippers, which comprised an additional 5–6% of the breeding population each year (Table 3).

Survival.—Apparent annual survival was highest among prebreeders (Table 3), which consisted primarily of younger birds. Survival was lower in successful breeders than in failed breeders, and the difference was larger in males (Table 3). Survival was similar in males and females among prebreeders, breeders, and failed breeders, but survival of males was lower among skippers (Table 3). None of the top models included a year effect on survival of prebreeders, breeders, or skipped breeders (Tables 1 and 2).

Encounter probability.—Variation among years in encounter probability of prebreeders was the strongest effect; inclusion

of this parameter caused the largest improvement in AIC_c (Tables 1 and 2). Encounter probability of prebreeders increased each year as a result of increased monitoring effort and additional monitoring techniques (Fig. 1). Encounter probability of prebreeders was slightly but consistently higher in females than in males and was correlated with the number of monitoring visits made to the colony each year ($r = 0.80$ and 0.89 , $P = 0.05$ and 0.02 in females and males, respectively). Before 2004, no nonbreeders were banded, so their encounter probability was zero. Starting in 2006, use of field-readable leg bands facilitated identification of individuals at a distance. In 2010, use of remote cameras with infrared motion-sensitive triggers allowed the highest encounter probability despite somewhat reduced effort. Encounter probability of successful and failed breeders was 1.0 every year. Encounter probability of skipped breeders was 1.0 every year because of how they were defined; observed skippers were, by definition, always observed, and unobserved skippers were revealed in a subsequent year when they returned to the colony.

Life-stage transitions.—Transition rates among life stages varied among years and in some cases differed between the sexes. Among prebreeders, the probability of recruiting into the breeding population by transitioning into either the breeder or failed-breeder state varied among years (Fig. 2) and was slightly higher, on average, in females than in males (Table 3). Most birds failed in their first breeding attempt and thus transitioned into the failed-breeder state. Only in 2006, when recruitment was highest, did more first-time breeders succeed rather than fail (Fig. 2). The low recruitment rate from 2003 to 2004 is not meaningful, because no prebreeders were banded before 2004 and, thus, recruitment could not be measured. The proportion of first-time breeders in the population averaged 21% from 2006 to 2010 and ranged from 16% to 27%.

Among breeders, the probability of skipping the next breeding season varied in several ways. First, probability of skipping differed between the sexes but also depended on breeding success. Among females, successful breeders were more likely than failed breeders to skip the next breeding season, but among males,

TABLE 1. Four-state models used to investigate survival (S), encounter probability (p), and transition probabilities (ψ) among prebreeders (P), breeders (B), failed breeders (F), and skipped breeders (S) in Laysan Albatrosses at Kaena Point, Oahu, Hawaii, 2003–2010. Each model contained a minimum of 20 parameters (4 for survival, 4 for encounter probability, and 12 for transitions among states), but four parameters were fixed at zero in all models because they were not biologically possible: ψ_{PS} , ψ_{BP} , ψ_{FP} , and ψ_{SP} . In each model, only parameters that were not constant across groups and years are shown, indicated by subscripts. Only models with a reasonable fit and those illustrating the process used to arrive at the best model are shown.

Model no.	Model	ΔAIC_c	Model likelihood	Number of parameters	Deviance
1	$\rho P_{yr} \psi BS_{yr} \psi FS_{yr}$	0	1	34	1,283.42
2	$SS_{sex} \rho P_{yr} \psi BS_{yr} \psi FS_{yr}$	0.88	0.64	35	1,282.11
3	$\rho P_{yr} \psi BS_{sex+yr} \psi FS_{yr}$	1.69	0.43	35	1,282.93
4	$\rho P_{yr} \psi BS_{yr}$	1.73	0.42	28	1,298.13
5	$\rho P_{yr} \psi P_{sex} \psi BS_{yr} \psi FS_{yr}$	1.76	0.42	35	1,282.99
6	$\rho P_{yr} \psi PB_{sex} \psi BS_{yr} \psi FS_{yr}$	2.18	0.34	35	1,283.41
7	$\rho P_{yr} \psi PB_{yr} \psi BS_{yr} \psi FS_{yr}$	2.26	0.32	40	1,272.50
8	ρP_{yr}	7.38	0.03	22	1,316.56
9	Simplest model—all constant	31.67	0	16	1,353.45

TABLE 2. Five-state models used to investigate survival (*S*), encounter probability (*p*), and transition probabilities (ψ) among prebreeders (P), breeders (B), failed breeders (F), skippers (S), and unobserved skippers (U) in Laysan Albatross at Kaena Point, Oahu, Hawaii, 2003–2010. Each model contained a minimum of 30 parameters (5 for survival, 5 for encounter probability, and 20 for transitions among states), but six parameters were fixed at zero in all models because they were not biologically possible: ψ PS, ψ PU, ψ BP, ψ FP, ψ SP, and ψ UP. In each model, only parameters that were not constant across groups and years are shown, indicated by subscripts. Only models with a reasonable fit and those illustrating the process used to arrive at the best model are shown.

Model no.	Model	ΔAIC_c	Model likelihood	Number of parameters	Deviance
1	$SS_{sex} \rho P_{yr} \psi PB_{yr} \psi BS_{yr} \psi BU_{yr} \psi FU_{yr}$	0	1	55	1,240.95
2	$\rho P_{yr} \psi PB_{yr} \psi BS_{yr} \psi BU_{yr} \psi FU_{yr}$	0.97	0.62	54	1,244.21
3	$SS_{sex} \rho P_{yr} \psi PB_{yr} \psi BS_{yr} \psi BU_{yr} \psi FU_{yr} \psi SF_{sex}$	1.27	0.53	56	1,239.93
4	$SS_{sex} \rho P_{yr} \psi PB_{yr} \psi BS_{yr} \psi BU_{yr} \psi FU_{yr} \psi UB_{sex}$	1.41	0.49	56	1,240.07
5	$SS_{sex} \rho P_{yr} \psi PB_{yr} \psi BS_{yr} \psi BU_{yr} \psi FU_{yr} \psi FS_{yr}$	1.47	0.48	61	1,228.56
6	$SS_{sex} \rho P_{yr} \psi PB_{yr} \psi BS_{yr} \psi BU_{yr} \psi FU_{yr} \psi FU_{sex}$	1.50	0.47	56	1,240.15
7	$SS_{sex} \rho P_{yr} \psi PB_{yr} \psi BS_{yr} \psi BU_{yr} \psi FU_{yr} \psi SB_{sex}$	1.66	0.44	56	1,240.32
8	$SF_{sex} SS_{sex} \rho P_{yr} \psi PB_{yr} \psi BS_{yr} \psi BU_{yr} \psi FU_{yr}$	1.86	0.39	56	1,240.52
9	$SS_{sex} \rho P_{yr} \psi PB_{yr} \psi BS_{yr} \psi BU_{yr} \psi FU_{yr} \psi PF_{sex}$	1.87	0.39	56	1,240.53
10	$SS_{sex} \rho P_{sex+yr} \psi PB_{yr} \psi BS_{yr} \psi BU_{yr} \psi FU_{yr}$	1.87	0.39	56	1,240.53
11	$SB_{sex} SS_{sex} \rho P_{yr} \psi PB_{yr} \psi BS_{yr} \psi BU_{yr} \psi FU_{yr}$	1.93	0.38	56	1,240.59
12	$SS_{sex} \rho P_{yr} \psi PB_{yr} \psi BS_{yr} \psi BU_{yr} \psi FU_{yr} \psi UF_{sex}$	1.99	0.37	56	1,240.64
13	$SS_{sex} \rho P_{yr} \psi PB_{yr} \psi BS_{yr} \psi BU_{yr} \psi FU_{yr} \psi BS_{sex}$	2.07	0.35	56	1,240.73
14	$SS_{sex} \rho P_{yr} \psi PB_{yr} \psi BS_{yr} \psi BU_{yr} \psi FU_{yr} \psi US_{sex}$	2.24	0.33	56	1,240.89
15	$SS_{sex} \rho P_{yr} \psi PB_{yr} \psi BS_{yr} \psi BU_{yr} \psi FU_{yr} \psi FS_{sex}$	2.24	0.33	56	1,240.90
16	$SS_{sex} \rho P_{yr} \psi PB_{sex+yr} \psi BS_{yr} \psi BU_{yr} \psi FU_{yr}$	2.29	0.32	56	1,240.95
17	$SS_{sex} \rho P_{yr} \psi PB_{yr} \psi BS_{yr} \psi BU_{sex+yr} \psi FU_{yr}$	2.30	0.32	56	1,240.95
18	$\rho P_{yr} \psi BS_{yr} \psi BU_{yr} \psi FU_{yr}$	3.01	0.22	48	1,259.87
19	$\rho P_{yr} \psi BS_{yr} \psi BU_{yr}$	10.19	0.01	42	1,280.46
20	$\rho P_{yr} \psi BS_{yr}$	22.12	0	36	1,305.60
21	ρP_{yr}	23.80	0	30	1,320.29
22	Simplest model—all constant	50.05	0	24	1,359.36

TABLE 3. Estimates (\pm SE) of demographic parameters in Laysan Albatrosses at Kaena Point, Oahu, Hawaii, 2003–2010, obtained from four-state models and from five-state models that incorporated a state for unobserved skipped breeders. Many parameters varied among years (see Figs. 2, 3, and 5); values in this table are from models in which estimates were constrained to be constant over time.

Parameter	Four-state model estimate		Five-state model estimate	
	Female	Male	Female	Male
Survival: prebreeders	0.985 \pm 0.011	1.0 \pm 0.0	0.995 \pm 0.007	0.997 \pm 0.013
Survival: breeders	0.955 \pm 0.019	0.928 \pm 0.026	0.942 \pm 0.020	0.922 \pm 0.026
Survival: failed breeders	0.970 \pm 0.016	0.975 \pm 0.020	0.954 \pm 0.017	0.972 \pm 0.020
Survival: skippers	0.976 \pm 0.027	0.860 \pm 0.090	0.973 \pm 0.027	0.833 \pm 0.088
Encounter probability: breeders	0.882 \pm 0.022	0.882 \pm 0.022	1.0 \pm 0.0	1.0 \pm 0.0
Encounter probability: failed breeders	1.0 \pm 0.0	1.0 \pm 0.0	1.0 \pm 0.0	1.0 \pm 0.0
Encounter probability: prebreeders	0.761 \pm 0.034	0.759 \pm 0.041	0.750 \pm 0.033	0.748 \pm 0.040
Transition: breeder–skipper	0.182 \pm 0.032	0.152 \pm 0.032	0.180 \pm 0.033	0.165 \pm 0.036
Transition: breeder–unobserved skipper	–	–	0.056 \pm 0.020	0.050 \pm 0.022
Transition: failed breeder–skipper	0.108 \pm 0.024	0.119 \pm 0.040	0.110 \pm 0.025	0.120 \pm 0.040
Transition: failed breeder–unobserved skipper	–	–	0.033 \pm 0.014	0.066 \pm 0.031
Transition: skipper–breeder	0.792 \pm 0.077	0.755 \pm 0.108	0.797 \pm 0.077	0.745 \pm 0.110
Transition: unobserved skipper–breeder	–	–	0.657 \pm 0.113	0.698 \pm 0.116
Transition: prebreeder–breeder or failed breeder	0.237 \pm 0.022	0.212 \pm 0.027	0.233 \pm 0.022	0.207 \pm 0.025

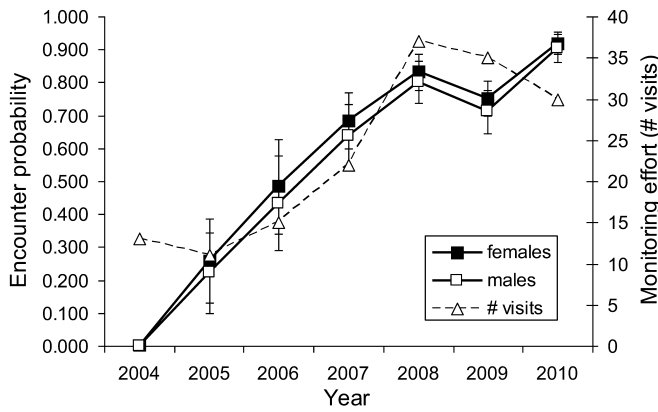


FIG. 1. Monitoring effort (visits per year) and encounter probability (\pm SE) of prebreeding Laysan Albatrosses at Kaena Point, Oahu, Hawaii, 2003–2010. Encounter probability was zero at first because no prebreeders were banded before 2004, then increased over time as monitoring effort increased. Use of remote cameras in 2010 allowed the highest encounter probability despite somewhat reduced effort.

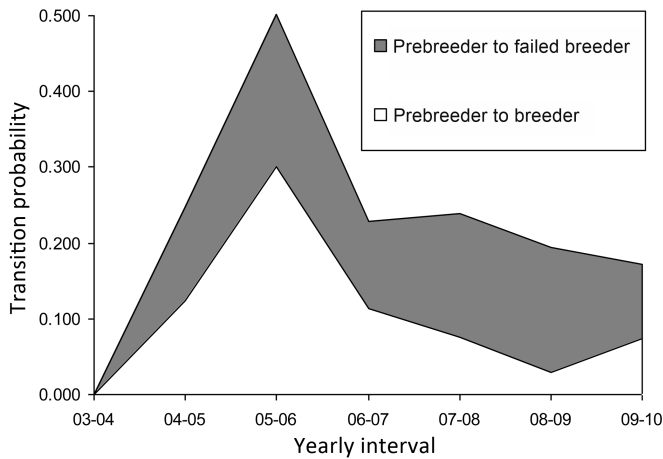


FIG. 2. Transition probability of Laysan Albatrosses at Kaena Point, Oahu, Hawaii, from prebreeder to breeder and failed breeder. Transition rates varied among years (2003–2010), and most birds failed in their first breeding attempt.

successful and failed breeders were equally likely to skip breeding the next year (Fig. 3). The average rate of skipped breeding in successful and failed breeders combined, obtained by weighting probability in each group by sample size, was slightly but not significantly higher in males (0.200 ± 0.032) than in females (0.187 ± 0.023). Second, the rate of skipping varied among years in successful breeders (Fig. 4A) and failed breeders (Fig. 4B). The true rate of skipped breeding was revealed by summing transition rates to observed and unobserved skippers (Table 3). The proportion of birds that skipped breeding yet were observed at the colony increased over time (Fig. 5), from zero in the first 2 years of the study when monitoring effort was low, to 100% in 2 of the last 4 years. Females occasionally skipped 2 years and one bird skipped 3 consecutive years, but males rarely skipped a second year.



FIG. 3. Transition probability (\pm SE) of female and male Laysan Albatrosses at Kaena Point, Oahu, Hawaii, 2003–2010, from breeder and failed breeder to skipper.

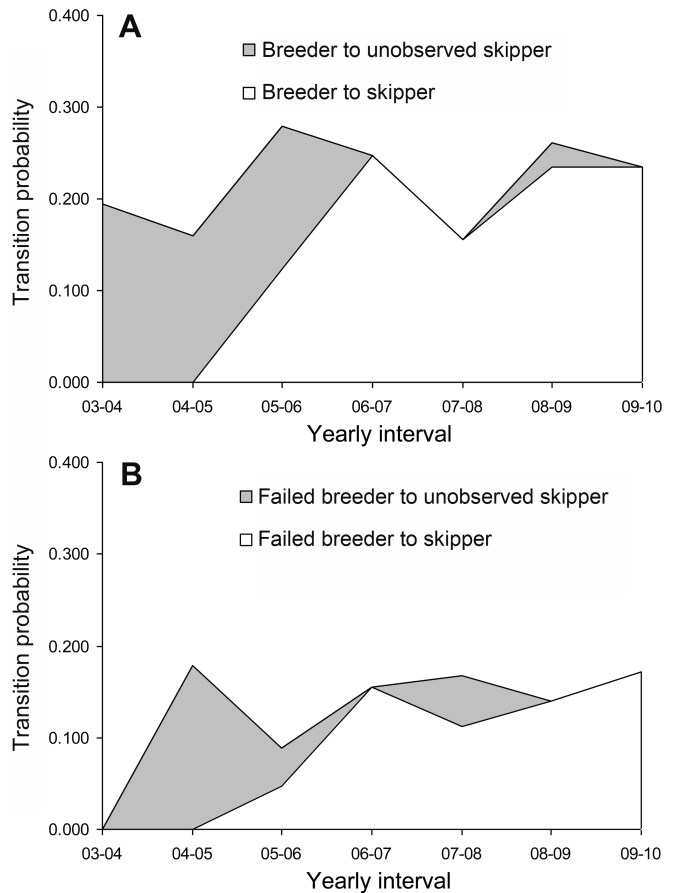


FIG. 4. Transition probability (for males and females combined, 2003–2010) of Laysan Albatrosses at Kaena Point, Oahu, Hawaii, from (A) breeder to skipper and unobserved skipper and (B) failed breeder to skipper and unobserved skipper. Successful breeders were more likely than failed breeders to skip the next breeding season. During the first 3 years of the study many skippers went undetected, but increased monitoring effort, use of field-readable bands starting in 2006, and use of remote cameras in 2010 resulted in most or all skippers being observed at the colony.

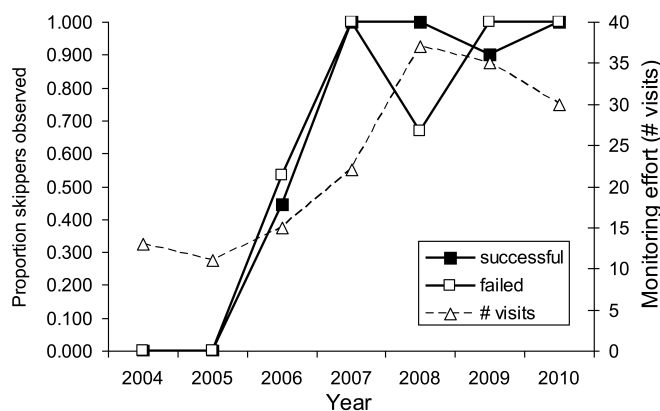


FIG. 5. Proportion of Laysan Albatrosses that skipped breeding yet were observed at the Kaena Point colony from 2003 to 2010. Proportion of skippers observed increased with number of visits per year and use of additional techniques, such as field-readable leg bands in 2006 and remote cameras in 2010.

DISCUSSION

Apparent survival.—Estimates of apparent annual survival in Laysan Albatrosses at Kaena Point were high, as expected for long-lived species. When estimates for successful and failed breeders were combined, the values for females (0.948) and males (0.947) were almost identical to those reported by Fisher (1975a) at Midway Atoll in 1960–1973 (females: 0.946, males: 0.947). The similarity in survival estimates is remarkable given the differences between studies in sample size (>27,000 vs. 249) and the earlier study's use of simple enumeration compared with our use of complex mark–recapture models. The most important similarity is that both studies involved populations that were stable or increasing. The size of the Midway colony was greatly reduced during World War II and by subsequent albatross control programs, but after those actions ceased in 1965 the number of birds grew during most of the time encompassed by Fisher's study (Arata et al. 2009). During our study from 2003 to 2010, Laysan Albatross numbers were generally stable overall (Arata et al. 2009), but the Kaena Point colony has been growing steadily since 1992 (Young et al. 2009b).

Estimates of adult survival in Laysan Albatrosses from the present study and Fisher's (1975a) were similar to estimates in other albatross species that were not experiencing significant mortality from bycatch in commercial fishing, which ranged from 0.93 to 0.98 (Verán et al. 2007: appendix S2). A breeding female from the Kaena Point colony was killed (and reported) by a Taiwanese long-liner in 2006, but the number of albatrosses killed by commercial fisheries in the central North Pacific, where most birds from the Kaena Point colony forage (Young et al. 2009a), has been greatly reduced since about 1993 (Cousins et al. 2000, Smith and Morgan 2005, Arata et al. 2009). By contrast, survival estimates were lower in several albatross populations that were declining (largely because of mortality of adults in fisheries bycatch), ranging from 0.84 to 0.92 (Weimerskirch and Jouventin 1987, Prince et al. 1994, Weimerskirch et al. 1997, Cuthbert et al. 2003, Arnold et al. 2006, Verán et al. 2007, Rivalan et al. 2010).

Survival of prebreeders (0.996 in males and females combined) was higher than that of breeders, and slightly higher than that reported by Fisher (1975a) for 4- to 8-year-old birds (0.982), which were roughly equivalent to our prebreeders. Prebreeders presumably had higher survival because they did not bear any cost of reproduction (Curio 1983, Bennett and Harvey 1988, Stearns 1992). Similarly, survival of successful breeders was lower than survival of failed breeders among males, which indicates a cost associated with the effort of raising a chick to independence. Among females, survival of successful breeders was not lower, but they were more likely than successful males to skip the next breeding season. In most mating systems, the cost of reproduction is higher in females than in males (Nur 1988), but in the Laysan Albatross this pattern depended on how far into the nesting cycle a pair progressed. The female incurs a substantial cost from laying an egg that comprises 9.5% of its body mass (Whittow 1993), regardless of how long it is incubated. Males bear a larger burden after the egg is laid because they take the first incubation shift, which is usually the longest at ≤ 32 days, and do 56% of the incubating (Rice and Kenyon 1962). At Kaena Point this difference in timing of reproductive effort was magnified because many nest failures occurred shortly after laying, in which case there was little cost to the male. Ekman and Askenmo (1986) also found that nonbreeding male Crested Tits (*Lophophanes cristatus*) had higher survival than males attending a brood, but Cubaynes et al. (2011) found that prebreeders had lower survival than adults in Red-footed Boobies (*Sula sula*).

Survival of Laysan Albatrosses did not vary among years, which supports predictions from life-history theory that long-lived species should respond to variable environmental conditions by adjusting their reproductive effort, including skipping breeding entirely, thereby buffering their own survival from such variation (Erikstad et al. 1998, Cubaynes et al. 2011). Indeed, skipped breeding and recruitment varied among years in the Laysan Albatross, which further supports this idea.

Survival of females that skipped breeding was high and similar to that of failed breeders, as expected given the lower reproductive effort of those groups, but survival of males that skipped breeding was much lower. It is possible that some males permanently emigrated from the study population, which would result in an underestimate of survival, but immigration to the colony has been female-biased (Young et al. 2008). This suggests that females are the more dispersant sex, which is typical of most bird species (Greenwood and Harvey 1982, Pusey 1987). Low survival of male skippers may indicate that they are more subject to threats, such as greater overlap of foraging range with fisheries and increased risk of mortality from bycatch (Fischer et al. 2009). Low survival of male skippers also could reflect a sexual dichotomy in the mechanism that regulates breeding frequency, similar to the different recruitment patterns of male and female Blue-footed Boobies (*S. neobouxi*) found by Oro et al. (2010).

Encounter probability.—Perhaps the most surprising result of our study was that prebreeders and skipped breeders visited the colony frequently. Albatrosses, sea turtles, and other marine animals in nonbreeding life stages have been assumed to remain at sea where they are unlikely to be encountered, which would constitute temporary emigration, leading to the use of unobservable states to estimate their survival (Kendall 2004, Converse et al. 2009, Kendall et al. 2009). Our results indicate that many prebreeders and virtually

all skipped breeders return to the colony each year. Fisher (1976) also documented skipped breeders visiting the colony at Midway and hypothesized that they did so to maintain a nesting territory, but he did not report the frequency at which they were encountered. The keys to discovering this at Kaena Point were (1) small colony size and ease of observing birds, (2) marking all nonbreeders with field-readable leg bands, and (3) increased monitoring effort and efficiency through more frequent visits and use of remote cameras at specific locations. We sometimes observed skipped breeders near their traditional nest sites, but more often they congregated in a few areas of the colony with other skippers and prebreeders. To obtain information about birds in unobservable states and mitigate bias in their survival estimates, Kendall et al. (2009) recommended (1) the use of buffer areas to detect movement of birds outside study plots and (2) telemetry, using satellite transmitters or data loggers, to directly track their status. Our results indicate that more focused monitoring, particularly using remote cameras in locations where nonbreeders congregate, is potentially more effective than buffer areas and less costly than telemetry.

Although the encounter probability of prebreeders and skipped breeders increased as monitoring improved, seemingly obviating the need for an unobservable state, we recommend continued use of this technique. We found that employing a separate state for unobserved skipped breeders improved estimates of survival and transition probability, as intended (Kendall and Nichols 2002, Kendall 2004). Changes over time in the proportion of unobserved skippers at Kaena Point helped us assess the efficacy of the monitoring design and variation in monitoring performance. Converse et al. (2009) also found that use of an unobservable state for successful breeders in the Grey-headed Albatross (*Thalassarche chrysotoma*), an obligate biennial breeder, improved estimates of survival and breeding frequency.

Life-stage transitions.—Transition of prebreeders into the breeding population was relatively high at Kaena Point, averaging 24% in females and 21% in males each year. The slightly higher recruitment of females was probably related to the high prevalence of female–female pairs in this colony (31%; Young et al. 2008). Some of these female–female pairs laid viable eggs (from extrapair copulations) and successfully reared offspring. Although the sex ratio was female-biased (1.5:1), which would seemingly favor male recruitment, females sometimes paired with each other and thus had more potential mates, whereas this option was not available to males. The proportion of first-time breeders in the population, another measure of recruitment, was similarly high, averaging 21% from 2006 to 2010. By contrast, Fisher (1976) measured the proportion of first-time breeders on Midway to be only 14% in 1960–1973. The higher recruitment at Kaena Point was probably attributable to lower density-dependent competition. Albatross population size and density were much higher on Midway, and Van Ryzin and Fisher (1976) found that age at first breeding was 8.6 years, with a modal age of 8 years and a few birds breeding as early as 5 years. At Kaena Point, preliminary data indicate that the age at first breeding was a year earlier, with an average of 7.7 years, a mode of 7, and one bird breeding in its fourth year (L. C. Young and E. A. VanderWerf unpubl. data), which is the earliest reported breeding age for this species. In the Wandering Albatross (*Diomedea exulans*), Croxall et al. (1990) and Weimerskirch et al. (1997) found that age at first breeding decreased as populations declined, presumably as a result of decreasing density-dependent competition. Long-term studies of several other seabirds have shown

evidence of density-dependent effects on recruitment rate and age at first breeding (Wooller et al. 1992).

Breeding frequency in Laysan Albatrosses at Kaena Point (0.807 ± 0.028 for males and females combined) was similar to previous estimates from Midway, though care was needed to interpret previous estimates because a range of values have been reported for different subsets of the breeding population. Rice and Kenyon (1962) found that breeding frequency was dependent on reproductive performance in the previous season, with rates ranging from 0.63 in birds that bred successfully to 0.87 in cases where the egg was infertile or failed early in incubation. When data from all groups were combined using the rate in each group weighted by its normalized sample size, the overall rate for the entire breeding population was 0.786. Breeding-frequency estimates from Fisher (1976) are sometimes cited as 0.82–0.86 or 0.84 ± 0.09 (e.g., Arata et al. 2009: table 11), but those values pertained only to experienced breeders that had a single mate for at least 10 years of the 13-year study. When data from all of Fisher's groups were combined, breeding frequency for the entire population was 0.757. In Grey-headed Albatrosses, breeding success greatly influenced whether a bird skipped a year of breeding, with 93.8% of successful breeders and 16.3% of failed breeders skipping the next year (Ryan et al. 2007, Converse et al. 2009).

Rates of recruitment and skipped breeding in Laysan Albatrosses at Kaena Point varied substantially among years, which suggests that these transitions were influenced by environmental conditions and were not simply a function of age. Fisher (1967) found that body mass was 8–11% lower in nonbreeding birds than in breeding birds and, assuming that albatrosses needed to reach a minimum body weight to attempt breeding, argued that breeding frequency was influenced by food availability. In Wandering Albatrosses, Weimerskirch (1992) found that breeders were heavier than nonbreeders of similar age and that only birds that attained a threshold value bred, regardless of age, which indicated that reproduction was constrained by body condition. In Red-footed Boobies, Cubaynes et al. (2011) found that skipped breeding was related to sea-surface temperature and was more likely during El Niño–Southern Oscillation events. Factors that influence recruitment and breeding frequency in Laysan Albatrosses warrant further investigation.

Jouventin and Dobson (2002) found that Laysan Albatrosses had above-average breeding frequency compared with other albatross species and classified them as annual breeders, primarily because their relatively small size and short developmental period allow a complete breeding cycle each year. Distance traveled during foraging trips may also influence breeding frequency by leading to less-frequent provisioning of offspring and slower development (Jouventin and Dobson 2002). Laysan Albatrosses indeed travel long distances to reach their primary foraging areas in the north Pacific (Hyrenbach et al. 2002, Young et al. 2009a, Kappes et al. 2010), but their offspring-provisioning rate was relatively high, so these long commutes did not appear to limit development or breeding frequency.

Accurate estimates of recruitment, breeding frequency, and their variation are important for obtaining reliable estimates of breeding population size because these parameters can cause substantial fluctuations in the number of birds that attempt to breed each year. Population sizes of Laysan and Black-footed albatrosses have been estimated primarily by nest counts, but because not all birds breed every year and this proportion varies among years, censuses of nesting birds alone do not provide a complete estimate

of the breeding population (Arata et al. 2009). Applying the average breeding frequency of 0.807 ± 0.028 to the 57 nests observed at Kaena Point in 2010 yields a breeding population estimate of 141 birds (95% confidence interval [CI]: 132–152). The accuracy of this estimate can be assessed by comparison with census data, which showed that 137 birds are known to have bred at Kaena Point in the past 3 years. Applying the same breeding frequency to the 408,130 nests counted at Midway in 2005 (Arata et al. 2009) yields a breeding population estimate of 1,011,475 birds (95% CI: 947,069–1,085,278). Because breeding frequency is slightly lower than is often reported in the literature, the true size of the Midway breeding population may be somewhat higher than is realized.

Although small and recently formed, the Kaena Point Laysan Albatross colony is similar in many ways to the larger colony on Midway and can be used to help answer questions about population dynamics, calculate population sizes, and measure efficacy of conservation actions. Several aspects of the Kaena Point system allowed us to overcome biases and estimate parameters that are difficult to measure at other locations. With data from additional years, we hope to examine survival and recruitment in juveniles and pre-breeders of different ages, the long-term effect of disease on survival (Young and VanderWerf 2008), and environmental factors that influence recruitment and breeding frequency. Kaena Point is one of a few Laysan Albatross breeding locations high enough to provide at least partial refuge from sea-level rise. Monitoring of this colony will contribute to knowledge about the effects of global climate change on the Laysan Albatross and other seabirds. Protection of this site will provide an alternative for many albatrosses and other birds that are likely to be displaced as their current breeding islands are inundated by rising sea level and surge from increasingly frequent and intense storms (Baker et al 2006).

ACKNOWLEDGMENTS

For field assistance we thank A. Titmus, A. Rudd, J. and H. Eijzenga, S. Plentovich, M. Hester, D. Hyrenbach, N. Yeung, and A. Stimpert. For permits to band albatrosses and work at Kaena Point we thank the Hawaii Natural Area Reserves System, the Hawaii Division of Forestry and Wildlife, the U.S. Fish and Wildlife Service, and the U.S. Geological Survey Bird Banding Laboratory. For technical advice on mark-recapture methods and use of Program MARK we thank P. Doherty and B. Kendall. This research was funded by the University of Hawaii (UH), Department of Zoology Jessie Kay Fellowship; several UH Ecology, Evolution, and Conservation Biology research awards as part of National Science Foundation grant DGE02-32016 to K. Kaneshiro; the David and Lucille Packard Foundation; and the Hawaii Audubon Society. The manuscript was improved by comments from two anonymous reviewers.

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Associate Editor: J. F. Piatt