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RESEARCH ARTICLE

Juvenile survival, recruitment, population size, and effects of avian pox virus in Laysan Albatross (*Phoebastria immutabilis*) on Oahu, Hawaii, USA

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ABSTRACT

Understanding population dynamics and determining conservation priorities in long-lived species with delayed breeding often is hampered by lack of information about younger age classes. Obtaining accurate estimates of juvenile survival and recruitment can be difficult because young individuals are infrequently observed. We used mark–recapture models to estimate age-specific survival, recruitment, population size, and encounter probability of Laysan Albatrosses (*Phoebastria immutabilis*) using a 14-yr dataset from Oahu, Hawaii, USA. We also measured the long-term effect of avian pox virus (*Poxvirus avium*) on the survival and recruitment of albatrosses infected as nestlings. Survival of juvenile albatrosses during the first year after fledging was 0.757 ± 0.042 . We were able to estimate juvenile survival, the first such estimate in any long-lived seabird, because our high search effort revealed that some birds began visiting the natal colony at the age of 1 yr. The survival of prebreeders increased rapidly and reached a value in the second year (0.973 ± 0.008) that was similar to the survival of breeding adults (0.973 ± 0.017). The average age of first return to the natal colony was 4.24 ± 0.11 yr. The average age at first breeding was 8.44 ± 0.15 yr, with recruitment probability peaking at ages 9–10 yr and a single bird being recruited into the breeding population at the age of 4 yr. Pox virus decreased survival in the first year by 4%–13% and decreased recruitment probability up to age 12 by 4%–26%, depending on the severity of infection. The total size of the Laysan Albatross population on Oahu in 2015 was 555 birds, consisting of 270 active breeders, 231 prebreeders, and 54 birds that likely skipped breeding that year. The number of prebreeders constituted an average of 44% of the total population. These demographic estimates will be useful for population modeling exercises involving various threat and management scenarios, and for examining environmental factors that influence demography.

Keywords: avian pox virus, Laysan Albatross, juvenile survival, mark–recapture, recruitment age

Supervivencia de las aves jóvenes, reclutamiento, tamaño poblacional y efectos del virus de la viruela en *Phoebastria immutabilis* en Oahu, Hawaii

RESUMEN

Entender la dinámica poblacional y determinar prioridades de conservación en especies longevas con reproducción lenta frecuentemente está limitado por la falta de información sobre las clases de edad más jóvenes. Obtener estimados precisos de la supervivencia de las aves jóvenes y el reclutamiento puede ser difícil debido a que los individuos jóvenes son difíciles de observar. Usamos modelos de marcado-recaptura para estimar la supervivencia específica de cada edad, el reclutamiento, el tamaño poblacional y la probabilidad de avistamiento de *Phoebastria immutabilis* usando un conjunto de datos de 14 años de Oahu, Hawaii. También medimos los efectos a largo plazo del virus de la viruela aviar (*Poxvirus avium*) sobre la supervivencia y el reclutamiento. La supervivencia de las aves jóvenes durante el primer año luego del emplumamiento fue 0.757 ± 0.042 . Pudimos estimar la supervivencia de las aves jóvenes, siendo éste el primer estimado de su tipo en aves marinas longevas, debido a que nuestro alto esfuerzo de muestreo reveló que algunas de las aves empezaban a visitar sus colonias natales a la edad de 1 año. La supervivencia de las aves antes de su reproducción incrementó rápidamente y al segundo año (0.973 ± 0.008) alcanzó un valor similar al de la supervivencia de los adultos reproductores (0.973 ± 0.017). La edad promedio del primer retorno fue 4.24 ± 0.11 años. La edad promedio de la primera reproducción fue 8.44 ± 0.15 años; la probabilidad de reclutamiento alcanzó su máximo entre 9 y 10 años y sólo un individuo reclutó a la edad de 4 años. El virus de la viruela redujo la supervivencia en el primer año entre 4 y 13%, y redujo la probabilidad de reclutamiento hasta la edad de 12 años entre 4 y 26%, dependiendo de la severidad de la infección. El tamaño total de la población de *P. immutabilis* en Oahu en 2015 fue 555 aves, incluyendo 270 aves reproductoras activas, 231 aves que aún no se habían reproducido y 54 aves que probablemente no se reprodujeron ese año. El número de aves que aún no se habían reproducido representó un 44% de la población total. Estos estimados demográficos serán útiles en ejercicios de modelamiento de la población que involucren varios escenarios de amenaza y manejo, y para examinar los factores ambientales que influyen en su demografía.

Palabras clave: edad de reclutamiento, marcado-recaptura, *Phoebastria immutabilis*, supervivencia de aves jóvenes, virus de la viruela aviar

INTRODUCTION

Understanding population dynamics in long-lived species is crucial for designing and implementing conservation strategies. Most demographic parameters can be estimated relatively easily for breeding adults, but obtaining information about other age classes often is more difficult. For species with delayed reproduction, estimating survival, recruitment, and population size of prebreeding individuals can be particularly problematic. After leaving their natal area, juvenile seabirds, salmon, and sea turtles may disperse over large ocean areas in which they are infrequently observed (Witham 1980, Crouse et al. 1987, Fay et al. 2015). The albatrosses (Diomedidae) provide a classic example, in which young birds traditionally have been thought to remain at sea continuously for their first several years after fledging (Tickell 2000, Brooke 2004).

Previous demographic studies of albatrosses have used indirect methods to infer survival during the first year after fledging or have estimated survival cumulatively over the first several years of life (Croxall et al. 1990, Weimerskirch 1992, Arnold et al. 2006, Rivalan et al. 2010). An improvement in this field was provided recently by Fay et al. (2015), who showed that Wandering Albatrosses (*Diomedea exulans*) began returning to the natal colony at 2 yr of age and used that information to estimate survival during the first 2 yr after fledging. Here, we show that a small percentage of Laysan Albatrosses (*Phoebastria immutabilis*) return to their natal colony at the age of 1 yr, further dispelling the assumption that all albatrosses remain at sea during their first several years, and providing a rare window into the first year of life in albatrosses.

Population size and trend are 2 of the most fundamental demographic parameters and often are used as primary measures of assessing a species' status (IUCN 2001). For albatrosses, sea turtles, and other long-lived species with delayed reproduction, measuring population size often is hindered by a lack of information about young animals that have not yet begun to breed (i.e. prebreeders), and such individuals may comprise a substantial portion of the population (Arata et al. 2009). Estimation of the population size of albatrosses is further complicated by the fact that they are not annual breeders, but skip breeding in some years (Fisher 1976, Jouventin and Dobson 2002). The frequency with which birds skip breeding varies among species depending on the length of the breeding cycle and within species depending on previous breeding experience, reproductive outcome in the previous year, food availability, and nutritional condition of individual birds (Fisher 1976, Weimerskirch 1992, Ryan et al. 2007, VanderWerf

and Young 2011). In this study, we provide direct estimates of the number of prebreeders in the Laysan Albatross population on the island of Oahu, Hawaii, USA, in each year, allowing estimation of the total annual population size. The Laysan Albatross population on Oahu is relatively new and small, but it is growing (Young et al. 2009), and its small size makes it an ideal system in which to investigate demographic issues that are less tractable in larger colonies.

Avian pox virus (*Poxvirus avium*) is an arbovirus that occurs virtually worldwide and has been reported in many different bird species (van Riper and Forrester 2007). The prevalence of avian pox virus varies greatly depending on a variety of environmental and host-specific factors, and the effect of the disease also varies among bird species. Some species exhibit strong immunity to pox virus and often recover, but species endemic to isolated oceanic islands, such as Hawaiian forest birds, have little immunity and can be crippled or killed by it (van Riper et al. 2002, Atkinson et al. 2005, VanderWerf et al. 2006). Pox virus infects a bird through a break in unfeathered skin or in the oral or respiratory mucous membranes, and can be transmitted by arthropod bites, contact with a contaminated surface, or aerosol particles (van Riper and Forrester 2007). The principal vector of avian pox virus in Hawaii is the introduced mosquito *Culex quinquefasciatus* (van Riper et al. 2002, Atkinson et al. 2005). Pox virus appears to be relatively rare in seabirds, but it has been reported in several species when they occur on human-inhabited islands that harbor mosquito vectors, including Laysan Albatrosses on Oahu and Midway, Hawaii (Young and VanderWerf 2008). We previously reported that most Laysan Albatross chicks on Oahu that were infected with pox virus survived to fledging, but that the long-term postfledging survival of those birds was unknown (Young and VanderWerf 2008).

We used a 14-yr dataset on Laysan Albatrosses that were banded as chicks on Oahu to investigate age-specific survival, recruitment, and encounter probability. Our specific goals were to: (1) estimate survival of juveniles in the first year after fledging and in subsequent age classes; (2) document the ages at which birds began returning to the colony and began breeding; (3) examine annual variation in survival and recruitment; (4) estimate the total size of the Laysan Albatross population on Oahu, including breeders and prebreeders; and (5) measure the long-term survival and recruitment of Laysan Albatrosses infected as chicks with pox virus. These estimates come at a crucial time, when almost all albatross species worldwide are under threat from a variety of factors and there is

debate about which conservation actions would be most cost-effective (Finkelstein et al. 2008, Arata et al. 2009, Żydelski et al. 2009, Lebreton and Véran 2013). The demographic estimates that we report here can help to better inform population assessments, demographic models, and selection of conservation actions by wildlife managers.

METHODS

Study Sites and Population

We studied Laysan Albatrosses nesting in 2 locations on Oahu: Kaena Point Natural Area Reserve and Kuaokala Game Management Area. Kaena Point is the westernmost tip of Oahu (21°58'N, 158°27'W) and the reserve 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, just 1 hr by road from urban Honolulu, and is open to the public at all times. Kuaokala is located 6 km east of Kaena Point at 350 m elevation in a remote location in the northern Waianae Mountains (21°56'N, 158°23'W). Both colonies are relatively new and small, but they have grown steadily from a single nest at Kaena Point in 1992 to a maximum of 135 nests in both colonies in 2015 (Young et al. 2009, L. Young and E. VanderWerf personal observations). Adult Laysan Albatrosses arrive on Oahu in November, lay eggs in late November and early December, and fledge chicks in June–July. A predator-proof fence was constructed at Kaena Point in 2011 to protect nesting seabirds and other natural resources (Young et al. 2013). Before 2011 at Kaena Point, alien mammalian predators, including feral cats (*Felis catus*), dogs (*Canis familiaris*), and small Indian mongooses (*Herpestes auro-punctatus*), were controlled but still present in reduced densities. At Kuaokala, the colony is protected by a hog-wire fence to keep out feral pigs (*Sus scrofa*) and dogs.

Data Collection

We monitored Laysan Albatrosses at Kaena Point and Kuaokala from 2002 to 2015 during the November to June breeding season. Each breeding season spanned 2 calendar years, so we referred to breeding seasons by the year in which chicks fledged. We marked all chicks at both sites in April or May each year, when they were 3–4 mo old and 1–2 mo before fledging, with a U.S. Geological Survey Bird Banding Laboratory (BBL) metal leg band with a unique serial number. We also banded any adults that were not already banded. Starting in 2006, we also marked all adults and chicks with a field-readable colored plastic leg band to allow identification of individual birds at a distance. During banding, we collected either a small (400 μ L) blood sample from the tarsal vein or a feather sample for genetic sexing and other genetic analyses. All individuals

were sexed following protocols in Fridolfsson and Ellegren (1999) and Young et al. (2008). If any chicks died after banding and did not fledge, we removed the bands and excluded them from the dataset.

We visited Kaena Point at weekly intervals and Kuaokala once or twice a month. During each visit we checked the band numbers of all birds on nests and we attempted to identify all other birds from a distance using binoculars. Because both colonies were small and birds were readily visible, we often identified or captured every bird present. However, as the colonies grew, more time was required to identify all birds. To assist with resighting color-banded birds, starting in 2010, we deployed remote cameras with infrared motion-sensitive triggers (various models made by Bushnell, Overland Park, Kansas, USA, or Reconyx, Holmen, Wisconsin, USA) in areas of each colony where nonbreeding birds congregated. We deployed 4 cameras at Kaena Point and 3 at Kuaokala.

On each visit we examined each chick for signs of pox virus, such as wart-like nodules and tumorous lesions on unfeathered body areas, including the feet, legs, face, and around the bill and eyes (Tripathy 1993). Clinical signs of the less common diphtheritic form, or wet pox, include soft yellowish cankers and lesions on membranes of the upper respiratory and digestive tracts and in the mouth (Tripathy 1993, van Riper and Forrester 2007). For each infected bird, we categorized the severity of infection as mild, moderate, or severe (Table 1) using the following definitions, and we took notes on severity progression over time: mild infections were characterized by a few small lesions or growths on the bill, eyes, face, or feet; moderate infections resulted in larger lesions that covered up to 50% of the face or bill but did not appear to inhibit vision or feeding; severe infections consisted of extensive lesions that completely covered one or both eyes, >50% of the face, or resulted in deformation of the bill or head. We regarded any instance of wet pox as a severe infection. It is possible that some chicks were infected with pox virus but did not exhibit sufficient signs to be diagnosed by gross examination. Clinical confirmation of the pox virus diagnosis was conducted at the U.S. Geological Survey Pacific Island Ecosystems Research Center in Volcano, Hawaii, using small (<2 \times 2 mm) samples of sloughing epithelial tissue that we collected from lesions on 2 chicks, and according to protocols outlined in Jarvi et al. (2008). The strain of virus infecting the 2 clinically diagnosed Laysan Albatross chicks was canary pox, the same strain found in Hawaiian forest birds (Jarvi et al. 2008).

Our dataset included 477 Laysan Albatrosses that we banded as chicks on Oahu from 2002 to 2015, of which 325 hatched at Kaena Point and 152 at Kuaokala. Laysan Albatross chicks that hatched on Oahu from 1992 to 2000 were banded by the Hawaii Division of Forestry and Wildlife ($n = 35$). We included these chicks in our analysis

TABLE 1. Number of Laysan Albatross chicks banded on Oahu, Hawaii, USA, by year and pox virus infection severity. Mild infections were characterized by a few small lesions or growths on the bill, eyes, face, or feet; moderate infections resulted in larger lesions that covered up to 50% of the face or bill but did not appear to inhibit vision or feeding; and severe infections consisted of extensive lesions that completely covered one or both eyes, >50% of the face, or resulted in deformation of the bill or head.

Year	Pox severity				Total
	None	Mild	Moderate	Severe	
2002	20	0	0	0	20
2003	31	0	0	0	31
2004	1	1	3	11	16
2005	0	3	8	12	23
2006	1	1	23	8	33
2007	39	0	0	0	39
2008	23	0	3	1	27
2009	1	7	5	11	24
2010	43	0	0	0	43
2011	0	3	7	7	17
2012	44	0	0	0	44
2013	41	0	0	0	41
2014	31	8	6	0	45
2015	74	0	0	0	74
Total	349	23	55	50	477

of recruitment age, but not in our mark–recapture analysis of survival because search effort for banded birds was lower before 2002. We often encountered birds that were banded at locations other than Kaena Point and Kuaokala and we reported these birds to the BBL, who provided information on their origin and age. Some of these birds were banded as chicks and were of known age ($n = 35$), but we did not include them in our dataset because such birds were more likely to have returned to their natal colony, and the search effort for them at other locations was unknown and likely to have been lower prior to their arrival on Oahu.

Data Analysis

We created an encounter history for each bird starting with the year in which it was banded and fledged and including all resightings in subsequent years. We used multistate models in program MARK 6.1 (White and Burnham 1999) to generate maximum-likelihood estimates of apparent annual survival (S), encounter probability (p), and the transition probability (ψ) between 2 states representing prebreeders (P), which were younger birds that had not yet begun to breed, and breeders (B). We used an age-specific and time-specific parameter structure. We used severity of pox infection at the nestling stage as an individual covariate, with severity converted to a numerical scale (no pox = 0, mild = 1, moderate = 2, severe = 3) to allow its use in MARK (Cooch and White

2005). Our survival estimates represent apparent survival because the population that we sampled was open and the fate of birds was unknown. It was not biologically possible for birds to revert from the breeder state back to the prebreeder state, so this transition probability was fixed at 0 in all models. This study encompassed a period of 14 yr (2002–2015), so there were 13 annual intervals. Model notation follows Lebreton et al. (1992), in which subscripts indicate whether parameters differed among age classes (S_{age}), years (S_{yr}), or pox severity categories (S_{pox}), or were constant (S).

We created a set of candidate models that included various parameters to examine patterns of biological interest, such as differences between age classes, years, or pox severity categories (Table 2). In addition to annual variation, we created a model in which survival of prebreeders during the first year after fledging (S_{age1}) differed from survival in all subsequent years (S_{2+}). 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. We performed a goodness-of-fit test on a global model (Table 2, Model 10) using the median \hat{c} approach in MARK. However, the median \hat{c} method does not work for models with individual covariates, so instead we estimated \hat{c} using the same dataset but without the pox severity covariate. The estimated value of \hat{c} was 1.26 ± 0.02 , which indicated that the data were overdispersed, so we adjusted \hat{c} to that value.

There were no significant differences between the Kaena Point and Kuaokala colonies in any demographic parameter that we measured, so we combined the data from both sites in all analyses. For example, the percentage of birds that returned to the colony in all years combined did not differ between Kaena (39%) and Kuaokala (37%; $\chi^2_1 = 0.20$, $P = 0.65$), and the average age at first return did not differ between Kaena Point (4.20 ± 0.13 yr, $n = 130$) and Kuaokala (4.33 ± 0.20 yr, $n = 57$; $t_{109} = -0.55$, $P = 0.58$). Similarly, the percentage of birds that were recruited into the breeding population did not differ between Kaena Point (15%) and Kuaokala (16%; $\chi^2_1 = 0.04$, $P = 0.85$), and the average age at first breeding also did not differ between Kaena Point (8.59 ± 0.20 yr, $n = 49$) and Kuaokala (8.13 ± 0.18 yr, $n = 23$; $t_{63} = 1.73$, $P = 0.09$).

We were forced to combine data from both sexes in mark–recapture analyses because the sex of 56 chicks was unknown and the sample size of known-sex chicks was small in some years. Instead, we used simple enumeration to calculate the percentage of males and females that had returned to the colonies thus far, and we tested whether return rates differed between the sexes with a chi-square test.

TABLE 2. Multistate models used to investigate survival of prebreeders (SP) and breeders (SB), encounter probability of prebreeders (pP) and breeders (pB), and transition probability of known-age Laysan Albatrosses from a prebreeding to a breeding state (ψPB) on Oahu, Hawaii, USA, from 2002 to 2015. Explanatory factors in the models include: severity of pox virus infection (pox), first-year vs. older age classes (age1), all age classes (age), time (yr), or none (.). Models were ranked by the difference from the top model in quasi-Akaike's Information Criterion corrected for small sample size ($\Delta QAIC_c$). Likelihood is the probability that a model is the best model given the data, and K is the number of model parameters.

Model #	Model	$\Delta QAIC_c$	Likelihood	K	Deviance
1	SP(pox + age1) SB(.) pP (age) pB (.) ψPB (age + pox)	0.00 ^a	1.000	35	1541.58
2	SP(pox) SB(.) pP (age) pB (.) ψPB (age + pox)	10.94	0.004	33	1556.82
3	SP(pox) SB(.) pP (age + pox) pB (.) ψPB (age + pox)	11.65	0.003	34	1555.38
4	SP(pox) SB(.) pP (age) pB (.) ψPB (age)	14.32	0.001	32	1562.34
5	SP(.) SB(.) pP (age) pB (.) ψPB (age)	16.66	<0.001	31	1566.82
6	SP(age) SB(.) pP (age) pB (.) ψPB (age)	23.85	<0.001	44	1545.87
7	SP(.) SB(.) pP (age) pB (.) ψPB (yr)	194.95	<0.001	30	1747.24
8	SP(.) SB(.) pP (age) pB (.) ψPB (age + yr)	213.03	<0.001	97	1611.75
9	SP(.) SB(.) pP (age) pB (.) ψPB (.)	222.68	<0.001	18	1800.22
10	SP(age + yr) SB(.) pP (age + yr) pB (.) ψPB (age + yr)	446.45	<0.001	252	1381.54
11	SP(.) SB(.) pP (.) pB (.) ψPB (.)	837.80	<0.001	5	2441.99

^a $QAIC_c = 1,614.25$.

It proved difficult to simultaneously examine age-specific and annual variation in survival and recruitment probabilities with mark–recapture methods due to sparse data in some years that resulted in inestimable parameters. Instead, we examined annual variation in recruitment age using a one-way analysis of variance, and we tested the correlation between mean annual recruitment age and annual recruitment probability.

We calculated the total size of the Laysan Albatross population on Oahu by adding estimates of the numbers of prebreeders, breeders, and breeders that skipped breeding. We calculated the number of prebreeders each year by dividing the number of individuals known to have been recruited into the breeding population by the recruitment probability estimate from program MARK. We measured the number of active breeders by conducting a census each year. We estimated the number of individuals that were likely to have skipped breeding each year by multiplying the number of active breeders by the average frequency of skipped breeding in this population, which was 20% (VanderWerf and Young 2011).

RESULTS

Model Performance

The best model (Table 2, model 1) included parameters representing the following factors: an effect of pox virus on the survival of prebreeders; an age-specific parameter in which the survival of prebreeders differed between the first year after fledging and all subsequent age classes; age-specific variation in the encounter probability of prebreeders; age-specific variation in the transition probability of prebreeders; and an effect of pox on the transition probability of prebreeders. Inclusion of other parameters

resulted in worse model fit, indicating that there was no effect of pox virus on the encounter probability of prebreeders (model 3 vs. model 1) and that the survival of prebreeders did not vary among age classes after the age of 1 yr (model 6 vs. model 5). The inclusion of a parameter representing annual variation in transition probability of prebreeders improved model fit (model 7 vs. model 9), indicating that there was variation among years, but the inclusion of both age-specific and time-specific factors caused the data to become too sparse and resulted in worse model fit (model 8), preventing annual variation in transition probability from appearing in the best model.

Survival

The survival of prebreeders was lower in the first year after fledging (0.757 ± 0.042) than in subsequent years (0.973 ± 0.008). Annual survival of breeders (0.973 ± 0.017) was very similar to that of prebreeders older than the age of 1 yr and did not vary among years. Survival in the first year after fledging was affected by pox severity; survival of uninfected birds was 0.778 ± 0.043 and estimates were progressively lower by 4%–13% in each more severe infection category (Figure 1). We were not able to estimate annual survival of males and females separately using mark–recapture models, but simple enumeration showed that the percentage of birds that had returned to the colonies thus far was similar between females (90 of 208 = 43%) and males (91 of 213 = 43%; $\chi^2_1 = 0.013$, $P = 0.91$).

Encounter Probability and Age at First Return

The probability of encountering a bird at the colony increased with age; in the first year after fledging the chance of observing a bird was just 2%, and the rate increased each year until a peak at the age of 8 yr, when

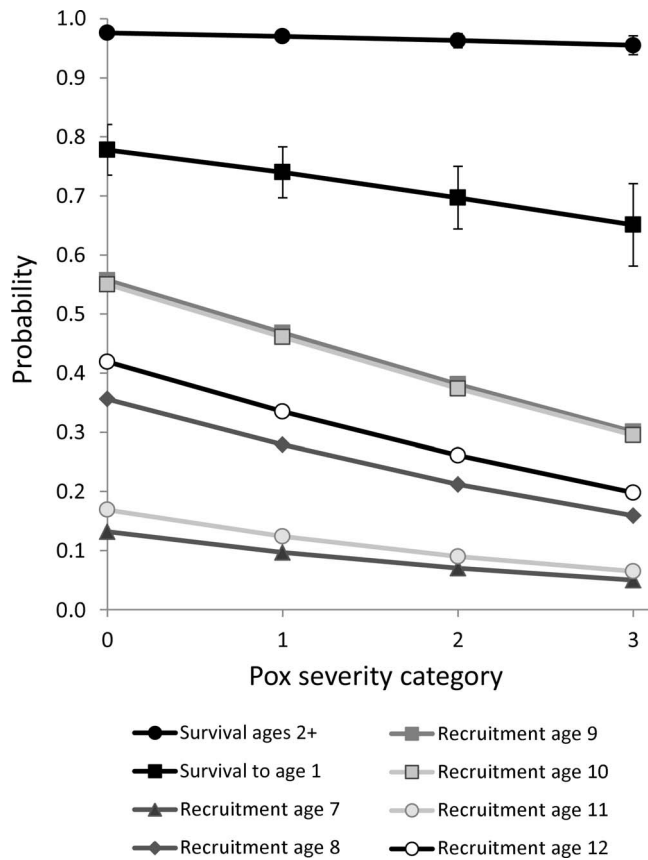


FIGURE 1. Effect of pox virus infection severity in Laysan Albatross nestlings on their subsequent survival and recruitment into the breeding population on Oahu, Hawaii, USA, from 2002 to 2015. Survival to age 1 yr was estimated separately from all subsequent ages until recruitment. Probability of recruitment was estimated by age class (7 to 12 yr old). Severity of pox virus infection was categorized as follows: 0 = none; 1 = mild; 2 = moderate; 3 = severe. Error bars are ± 1 SE.

there was a 92% chance of encountering a bird that was alive (Figure 2). After the age of 10 yr most birds had been recruited into the breeding population, died, or permanently emigrated, and the encounter probability of the remaining prebreeders declined and became more variable. The average age of first return to the natal colony was 4.24 ± 0.11 yr ($n = 187$), with a few birds returning at the age of 1 yr (Figure 3). The identity of several 1-yr-olds was documented with photographs taken by remote cameras. There was no difference in the age at first return between females and males (4.33 ± 0.17 yr vs. 4.12 ± 0.16 yr, respectively; $t_{178} = 0.94$, $P = 0.35$).

Recruitment Probability, Recruitment Age, and Population Size

The probability of a bird transitioning from the prebreeding state to the breeding state, or of being recruited, was 0 during the first 3 yr after fledging and very low during yr

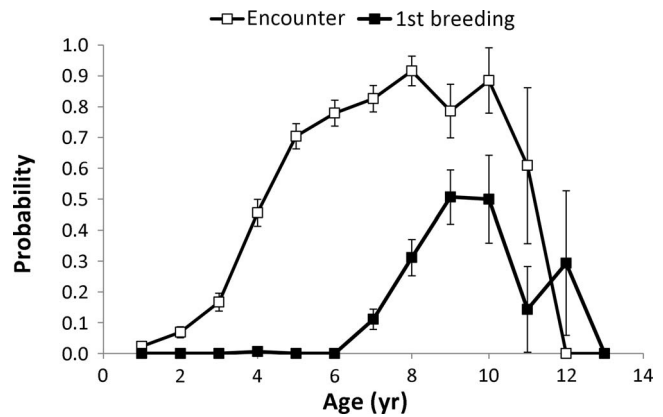


FIGURE 2. Age-specific probabilities of Laysan Albatrosses being encountered at the colony and being recruited into the breeding population on Oahu, Hawaii, USA, from 2002 to 2015. Error bars are ± 1 SE.

4–6 (Figure 2). Recruitment probability peaked at ages 9–10 yr and declined thereafter, and all birds had been recruited, died, or permanently emigrated by the age of 13 yr (Figure 2).

The average age at first breeding, or recruitment age, was 8.44 ± 0.15 yr, and the youngest age at first breeding was 4 yr ($n = 73$; Figure 3). Age at first breeding was correlated with age at first return ($r = 0.42$, $P < 0.001$; Figure 4). There was no difference in recruitment age between females and males (8.70 ± 0.25 yr vs. 8.23 ± 0.16 yr, respectively; $t_{55} = 1.56$, $P = 0.13$). Pox virus infection reduced recruitment probability at all ages, with recruitment progressively lower in each more severe infection category and reductions in recruitment of 4%–26% (Figure 1).

Recruitment probability varied among years, with an exceptionally high value in 2015 and a smaller peak in 2012 (Figure 5). Recruitment age also exhibited annual variation ($F_{6,65} = 4.16$, $P = 0.001$) and increased over time ($F_{1,5} = 8.55$, $P = 0.03$), with younger average recruitment



FIGURE 3. Ages of Laysan Albatrosses hatched on Oahu, Hawaii, USA, at first return to the colony and at recruitment into the breeding population, from 2002 to 2015.

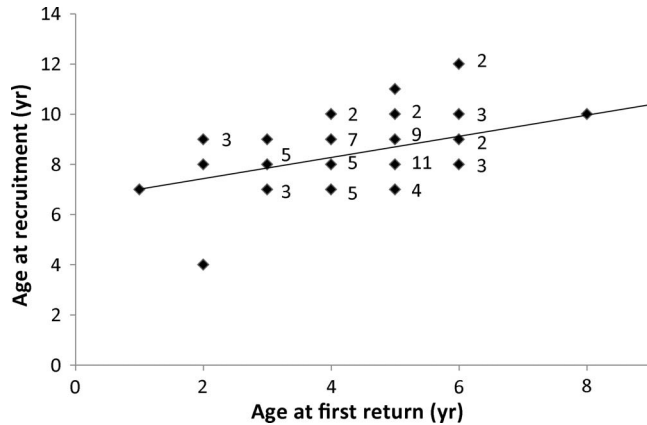


FIGURE 4. Relationship between age at first return to the natal colony and age at first breeding for Laysan Albatrosses hatched on Oahu, Hawaii, USA, with least-squares regression line. Many points represent multiple individuals; numbers to the right of points indicate sample size, and total sample size = 73.

ages during the earlier part of the study, but there was no correlation between recruitment probability and mean recruitment age ($r = 0.28$, $P = 0.55$).

The total estimated size of the Laysan Albatross population on Oahu in the most recent year of the study, 2015, was 555 birds, including 231 prebreeders, 270 active breeders, and 54 birds that likely had skipped breeding in that year. The number of prebreeders, calculated from recruitment probability and the number of recruits each year, was consistently similar to the number of active breeders, and constituted 44% of the total population on average (Figure 6).

DISCUSSION

Survival

In this study, we provide the first direct estimate of juvenile survival during the first year after fledging for a long-lived seabird. This adds to the recent improvement in understanding of albatross demography provided by Fay et al. (2015), who estimated survival in the first 2 yr after fledging to be 0.801 for the Wandering Albatross. We were able to obtain an estimate for the first year because our high search effort revealed that birds began visiting the natal colony at the age of 1 yr. Using the value for Laysan Albatrosses that were not infected with pox virus (0.778), juvenile survival of Laysan Albatrosses in their first year was similar to that of Wandering Albatrosses during the first 2 yr of life, despite large differences in sample sizes and study durations ($n = 9,685$ and 48 yr for Wandering Albatross; $n = 477$ and 14 yr for Laysan Albatross). However, Fay et al. (2015) found that survival of Wandering Albatrosses remained relatively low during yr 3–8 (0.918) and then increased to an adult value in yr 9–13

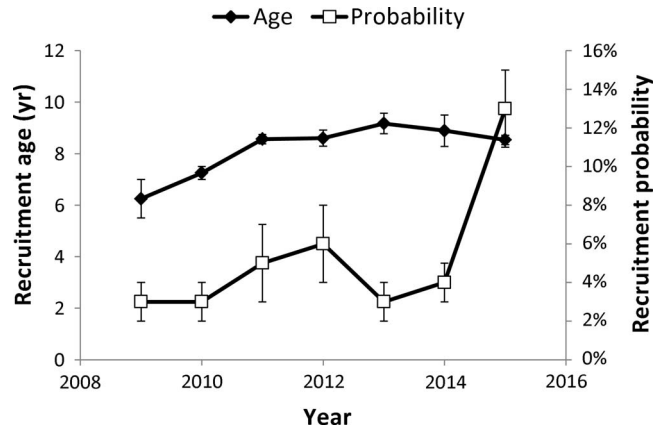


FIGURE 5. Relationship between annual variation in recruitment age and recruitment probability for Laysan Albatrosses on Oahu, Hawaii, USA, from 2009 to 2015. Error bars are ± 1 SE.

(0.980), whereas for Laysan Albatrosses, survival increased more rapidly to an adult value in yr 2 (0.973) and remained constant thereafter.

Other valuable information about postfledging survival in albatrosses has been obtained from tracking studies in which satellite transmitters were attached to juveniles just before fledging. Deguchi et al. (2014) found that survival of hand-reared and naturally reared Short-tailed Albatrosses (*Phoebastria albatrus*) was 85% during the first 9 days after fledging. Alderman et al. (2010) found that 13 of 48 Shy Albatrosses (*Thalassarche cauta*) fitted with satellite transmitters failed to fledge from the colony, and that 25 of the 35 fledglings (71%) survived for at least 10 days. Mortality shortly after fledging was higher for female than male Short-tailed Albatrosses (Deguchi et al. 2014), but did not differ between the sexes in Shy Albatrosses (Alderman et al. 2010). The results of both of these studies indicate

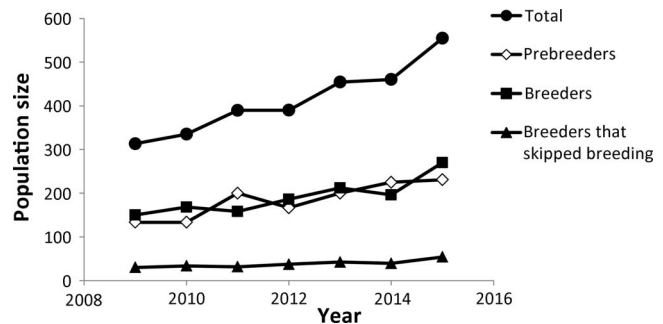


FIGURE 6. Laysan Albatross population size through time on Oahu, Hawaii, USA. Numbers of prebreeders were calculated from annual estimates of recruitment probability and number of birds recruited each year. Numbers of breeders were based on annual censuses and taken in part from Young et al. (2009). Numbers of breeders that did not breed (skipped breeding) in a particular year were taken in part from VanderWerf and Young (2011).

that most juvenile mortality occurs shortly after fledging, when birds are learning to develop flight and foraging skills.

These age-specific survival estimates can be used to improve population modeling exercises involving various threat and management scenarios, which previously have relied on indirect estimates inferred from other parameters (Wilcox and Donlan 2007, Finkelstein et al. 2008) or cumulative estimates from the first several years after fledging (Véran et al. 2007, Žydelas et al. 2009). For example, using an indirect method, Lebreton and Véran (2013) obtained an estimate of survival for Black-footed Albatrosses (*Phoebastria nigripes*) in their first year that was substantially lower (0.654 ± 0.051) than our estimate for Laysan Albatrosses. Because the survival of juvenile Laysan Albatrosses, and perhaps Black-footed Albatrosses, appears to be higher than previously recognized, management actions that protect breeding colonies and result in higher reproduction, such as predator control or eradication, may be more effective than previous modeling efforts have suggested (Wilcox and Donlan 2007, Finkelstein et al. 2008).

We previously found that annual survival of adult Laysan Albatrosses in the Kaena Point colony averaged 0.948 (VanderWerf and Young 2011), and that survival was higher for failed breeders (0.954 for females and 0.972 for males) than for successful breeders (0.942 for females and 0.922 for males). The adult survival estimate from the present study for both sexes combined (0.973) was more similar to that of failed breeders because the dataset was limited to younger birds that had been recruited recently, which often failed at nesting. Adult survival has been estimated for most albatross species, with annual rates ranging from 0.84 to 0.92 in declining populations under threat from fishing bycatch and from 0.91 to 0.98 in populations not threatened by fishing (Véran et al. 2007). Our survival estimates are in accord with the overall stable population trend of this species and the recent growth of the Oahu colonies (Arata et al. 2009, Young et al. 2009).

Age at First Return, Recruitment, and Population Size

Albatrosses traditionally have been thought to remain at sea continuously after fledging and to not return to the natal colony until several years of age (Tickell 2000, Brooke 2004). More recent information has dispelled this idea; we now know that some individuals begin returning to their natal colony when quite young. In Wandering Albatrosses, Fay et al. (2015) observed some 2-yr-olds at the natal colony. In Laysan Albatrosses, we found that at least 2% of birds first returned as 1-yr-olds, 7% as 2-yr-olds, and 17% as 3-yr-olds. Prebreeders may visit the colony infrequently at first and appear to spend more time at the colony as they age, so detecting the presence of the youngest birds requires substantial search effort. In our case, this involved

thorough searches of the entire colony on weekly visits throughout the nesting season (up to 37 visits per year) and the use of remote cameras with motion-sensitive triggers to supplement direct observations. Fisher and Fisher (1969) observed a few 2-yr-old Laysan Albatrosses on Midway, but did not detect any yearlings.

The recruitment ages of Laysan Albatrosses in this study were generally similar to those found in previous studies of Laysan Albatrosses on Midway (Fisher and Fisher 1969, Van Ryzin and Fisher 1976). The median age of recruitment for both sexes combined was 8 yr on both islands, the mean was 8.4 yr on Oahu and 8.6 yr on Midway, and the mean tended to be slightly higher for females than for males (8.7 ± 0.3 vs. 8.2 ± 0.2 yr on Oahu, 8.9 vs. 8.4 yr on Midway; Van Ryzin and Fisher 1976). Recruitment probability on Oahu increased with age to yr 10 and then declined, with 90% of birds having been recruited by 12 yr of age. The youngest age at first breeding on Midway was 5 yr for females and 6 yr for males (Van Ryzin and Fisher 1976). The 4-yr-old female that we found breeding at Kaena Point in 2009 is the youngest known breeder in any albatross species.

In the closely related Black-footed Albatross, the probability of recruitment has been reported to be substantially higher at younger ages than in the Laysan Albatross, e.g., 0.022 ± 0.006 at 5 yr of age, 0.290 ± 0.026 at 6 yr of age, and constant at 0.569 ± 0.042 at ages 7 yr and above (Véran et al. 2007, Lebreton and Véran 2013). These higher rates and lack of age-specific variation are surprising, given that these species are demographically similar in most other respects (Arata et al. 2009). Age at first breeding is generally related to body size in procellariiform seabirds (Bradley and Wooller 1991), with younger average recruitment ages in smaller species such as Manx Shearwater (*Puffinus puffinus*; 5 yr of age; Perrins et al. 1973), Christmas Shearwater (*Puffinus nativitatis*; 4 yr of age; VanderWerf et al. 2015), and Short-tailed Shearwater (*Ardenna tenuirostris*; 6–7 yr of age; Bradley et al. 1999), and older recruitment ages in larger species such as Wandering Albatross (10.9 yr for females, 11.4 yr for males; Croxall et al. 1990), Amsterdam Island Albatross (*Diomedea amsterdamensis*; 9.4 yr; Rivalan et al. 2010), and Northern Royal Albatross (*D. sanfordi*; 8.5 yr for females and 8.7 yr for males; Robertson 1993).

The increase in recruitment age over time in Laysan Albatrosses on Oahu is not likely to have been related to colony size or density dependence. The Kaena Point and Kuaokala colonies both increased in size during the study period (Young et al. 2009), but the population size on Oahu is still small and neither colony appears crowded compared with the very large colonies on Midway and Laysan, Hawaii. Furthermore, Fay et al. (2015) found that the recruitment probability of Wandering Albatrosses was positively correlated with population size; if this were true

for Laysan Albatrosses, it would have resulted in decreasing recruitment age over time.

Even in the year with the highest recruitment probability, the percentage of Laysan Albatross prebreeders that was recruited into the breeding population was relatively low, just 13%, demonstrating that there was a large pool of prebreeders. We previously reported that the annual recruitment probability of Laysan Albatrosses on Oahu averaged 25% for females and 21% for males (VanderWerf and Young 2011). Our previous estimates of annual recruitment were higher because they included birds that immigrated from other islands, which likely were older on average and thus more likely to be recruited. The number of prebreeders in the Oahu population increased over time because the growing number of breeders produced larger cohorts of offspring each year that joined the prebreeding pool (Figure 6). The number of prebreeders also reflected annual variation in recruitment probability. For example, low recruitment rates in 2009 and 2010 led to an accumulation of prebreeders in 2011, and then 2 yr of higher recruitment in 2011 and 2012 resulted in an increase in breeders and temporary depletion of prebreeders.

Prebreeders comprised a large percentage of the total Laysan Albatross population on Oahu, averaging 44% per year (range: 40%–51%). In the Short-tailed Albatross, it was gradual recruitment from such a pool of prebreeders that saved the species from extinction after virtually all of the breeding birds were killed by feather collectors in the early 1900s (Hasegawa and DeGange 1982). Our estimate of the total Laysan Albatross population on Oahu is the first such estimate for any albatross population because it includes active breeders, breeders that skipped breeding, and prebreeders. We were able to estimate these parameters because the Laysan Albatross colonies on Oahu are small and our monitoring effort was high; obtaining this type of information for larger colonies such as the one on Midway would be virtually impossible. The percentage of prebreeders in the Oahu population may be slightly higher than that in some larger albatross populations because the Oahu population is growing and larger cohorts enter the population each year. Our estimate of the Laysan Albatross population on Oahu may be an underestimate because it does not include prebreeders that immigrate from other islands. However, including such birds could result in an overestimate of the global Laysan Albatross population because they also may be visiting colonies on other islands, particularly their natal islands, and are best included in estimates from those islands until they actually select a breeding site.

Pox Virus

Laysan Albatrosses have strong immunity to pox virus and most infected chicks recover and fledge (Young and

VanderWerf 2008). However, after having followed chicks for up to 13 yr after fledging, we can now report that birds infected with pox virus as chicks show reduced survival and recruitment probability, and that the reductions are related to the severity of infection. The effect of pox virus on survival occurred only during the first year after fledging, but the effect on recruitment probability persisted much longer. Birds that had pox virus as chicks exhibited reduced recruitment probability compared with uninfected chicks even 12 yr after they appeared to have recovered, suggesting that they were either less able to attract a mate or less able to acquire the nutritional resources required for breeding, or both. Either way, pox virus infection resulted in substantial loss of lifetime fitness through reduced survival and reduced reproduction. Kleindorfer and Dudaniec (2006) also reported reduced pairing success in male Small Ground-Finches (*Geospiza fuliginosa*) infected with pox virus in the Galapagos Islands. Pox virus has been documented in Laysan Albatrosses in the small colonies on Oahu and Kauai, Hawaii, and locally near mosquito breeding sites on Midway, but pox virus currently is not considered a serious threat to the species. However, as the larger colonies on remote atolls face increasing threat from inundation associated with sea level rise and storm surge caused by climate change (Baker et al. 2006, Reynolds et al. 2015), colonies on higher islands such as Oahu, where mosquitoes are more widespread, may become more important to the conservation of the species, thereby increasing the importance of pox virus as a threat and the need to understand the demographic effects of this disease.

Conclusions

The Laysan Albatross population on Oahu is demographically very similar to the population on Midway in the 1960s (Fisher and Fisher 1969, Fisher 1975a, 1975b). The only demographic difference between the colonies discovered thus far is that the small colonies on Oahu and Kauai contain an unusually large number of female–female pairs, likely because of sex-biased immigration (Young et al. 2008, Young and VanderWerf 2014). These same-sex pairs have lower reproductive success than male–female pairs because they more often lay infertile eggs and more frequently abandon eggs shortly after laying, but this does not appear to influence survival and recruitment rates at the population level, which are similar to those on Midway. Analysis of more recent demographic data from Midway would help to demonstrate whether any other differences currently exist between large colonies and smaller, more recently established colonies, such as those on Oahu. Until more recent estimates from other colonies become available, our estimates are the best available information for use in modeling exercises for albatross populations in the North Pacific and for selecting the management options that are likely to be most cost-effective.

Variation in oceanographic conditions can have complex effects on the demography of long-lived seabirds. Fay et al. (2015) showed that the survival and recruitment of Wandering Albatrosses were influenced by oceanographic conditions, particularly sea surface temperature, and Oro et al. (2010) showed that there were complex interactions among climatic factors and age-specific survival and recruitment in Blue-footed Boobies (*Sula nebouxi*). The reproductive success of Laysan Albatrosses was recently shown to vary with oceanographic parameters, particularly sea surface temperature (Thorne et al. 2015). It is desirable to examine relationships between oceanic conditions and the survival and recruitment of Laysan Albatrosses, but in this study it proved difficult to simultaneously examine age-specific and time-specific variation in demographic parameters because of small sample sizes in some years. Recruitment age and recruitment probability both varied among years in this study, but there did not appear to be a relationship between these 2 parameters. Although the duration of our study (14 yr) was long by most standards, because of the delayed breeding and long lifespans exhibited by albatrosses, an even longer time series may be needed to adequately examine the complex interannual factors that affect whether Laysan Albatrosses attempt to begin breeding.

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Author contributions: E.A.V. and L.C.Y. conceived the ideas and collected the data; L.C.Y. compiled the data; and E.A.V. designed the methods, analyzed the data, and wrote the paper.

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