Survival of Laysan Teal *Anas laysanensis* differs between island populations: role of chronic avian botulism

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Abstract

Monitoring demographic response over time is valuable for understanding population dynamics of endangered species. We quantified the variation in survival patterns for three small isolated island populations of endangered waterfowl in the Hawaiian archipelago. Laysan Teal *Anas laysanensis* were individually marked and the fate of 1,150 individuals were followed from different cohorts among the two reintroduced (Kure and Midway Atolls) and the single relict (Laysan Island) populations for time series of 4, 10 and 15 years, respectively. We applied a non-parametric Kaplan-Meier estimator to describe variation between the populations in survival for different cohorts. For Laysan Island and Midway Atoll, we used log-rank tests to determine the effects of cohort, island and sex on survival. Birds in the Laysan Island population had significantly higher survival than those in the Midway population, and males had higher survival than females in both populations. The proportion of females surviving at Midway Atoll was 40% lower than for females on Laysan Island at year 5. The oldest bird observed from Laysan Island was at least 15.5 years old and had been ringed as an adult. The Kure Atoll founder cohort (*n* = 28) had 100% survival 18 months post-release, but this dropped by 39% during the first avian botulism type C outbreak. Ten of twenty-eight founders and a population of 60–70 birds persisted on Kure Atoll in 2020. We summarised mortality records to generate hypotheses to explain the cause-specific mechanisms driving the observed survival differences. Mortality data showed that the survival differences between islands in Laysan Teal survival was driven by chronic epizootics of avian botulism type C at Midway and Kure Atoll.

Key words: island endemic, Kaplan-Meier, Kure Atoll, Laysan Island, Midway Atoll, reintroduction, survival.

Island wildlife populations are sensitive to new threats intensified by changing climate, particularly increasing temperatures, storm intensity with sea level rise, and increased risk of disease (Devictor *et al.* 2008; Atkinson & LaPointe 2009; Reynolds *et al.* 2015). For the critically endangered populations of Laysan Teal *Anas laysanensis* (also called Laysan Duck) in the Hawaiian Islands it is important to detect and determine the cause and magnitude of mortality events because these may differ over time or between populations. Disease outbreaks, natural disasters, or management actions may increase risks to endangered species and decrease survival but threats may not be the same across the islands (Akçakaya & Ginzburg 1991; Reynolds *et al.* 2017a; USFWS 2019).

Previously widespread in the islands of the Hawaiian archipelago, Laysan Teal were extirpated from the main islands *c.* 800 years ago, coinciding with the arrival of non-native rats R*attus* sp. and by 1850 they persisted only on Laysan and Lisianski islands (Olson & James 1991; Olson & Ziegler 1995; Cooper *et al.* 1996; Burney *et al.* 2001). Although Laysan Teal can fly, today they do not migrate or disperse from Laysan Island, where there are no mammalian predators. The species came to the brink of global extinction following the introduction of the European Rabbit *Oryctolagus cuniculus* which denuded Laysan Island of vegetation by around 1903, when fewer than 20 Laysan Teal were counted (Dill & Bryan 1912). Following elimination of the rabbits by 1925, the Laysan Teal population increased over several decades to more than 500 individuals (Warner 1963), which was close to the carrying capacity of the island (Seavy *et al.* 2009). The species was listed as Endangered in 1967 (US Endangered Species Act [ESA 1973, as amended; USFWS 1976]) because of its small population size and total range (then only approximately 4 km^2).

The species' vulnerability to anthropogenic and natural disasters and to climate change has been identified as a threat in the Laysan Duck Recovery Plan and U.S. Geological Survey (USGS) climate change vulnerability assessments (USFWS 2009; Reynolds *et al.* 2012b). To lessen the risk of extinction from random disasters, a population was reintroduced using wild to wild translocation from Laysan Island to Midway Atoll during 2004–2005, and a second reintroduction attempt from Midway Atoll to Kure Atoll was made in 2014 (Reynolds & Klavitter 2006; Reynolds *et al.* 2008; USFWS 2009; Walters & Reynolds 2013; PNMN 2014). These translocations to other small low lying isolated islands in the Hawaiian archipelago (total range now *c.* 11 km^2) do not meet the criteria for recovery of the species (USFWS 2009) nor do they eliminate its extinction risks. However, the probability of persistence was increased since the number of island populations greatly influences a species' extinction likelihood (*e.g.* three populations are safer than one; Melbourne & Hastings 2008; Reynolds *et al.* 2013b).

At Midway Atoll early post-release annual survival ($\hat{S}$) was high for translocated founders, $\hat{S} = 0.92$ (s.e. = 0.019; $n = 42$) and their offspring, $\hat{S} = 0.82$ (s.e. = 0.008; $n = 67$) (Reynolds *et al.* 2008). These survival estimates, from the first two years post-release (2004–2006) were similar to adult survival estimates for the Laysan Island population where annual survival ranged from 0.88–0.91 (s.e. = 0.017–0.019; *n* = 355) during 1998–2004 (Reynolds & Citta 2007). However, four years post-release, the Midway population experienced its first epizootic of avian botulism type C, with over 180 carcasses collected during a 3-month period (Work *et al.* 2010). Subsequent habitat changes (landscape-scale herbicide application for weed removal), catastrophic sudden flooding from the 2011 Tohoku Tsunami and chronic, annual botulism outbreaks, were concurrent with increased carcass detection and Laysan Teal population declines (Reynolds *et al.* 2017a,b).

Avian botulism is the most common disease in wild birds worldwide (Rocke & Bollinger 2007). The frequency of avian botulism epizootics may increase globally with climate change due to warmer weather, more extreme storms and sudden flooding (Espelund & Klaveness 2014; Reynolds *et al.* 2017a,b). The bacteria that produces the toxin, *Clostridium botulinum,* favours high temperatures for growth (optimally 37°C) and may outcompete other inhibitory bacteria in effluent, eutrophic or herbicide-laden environments – *e.g.* those treated with glyphosate (Sandler *et al.* 1998; Krüger *et al.* 2013; Shehata *et al.* 2013; Vidal *et al.* 2013). Many large, avian botulism epizootics are associated with extreme droughts or sudden flooding that mobilise spores, leave carcasses, and create other conditions favourable for toxigenesis (Reynolds *et al.* 2017b; Son *et al.* 2018). Non-migratory island endemic waterbirds will have high exposure to this lethal food-borne paralytic toxin because of their limited habitat and limited dispersal from infected areas.

In this study, we quantified survival rates for individually marked birds from the three island populations and tested for evidence of differences in survival in relation to islands, cohorts (capture year), and sex for two of the populations. To help to understand differences in survival, we also summarised longevity and mortality records and estimated average annual survival for the three demographically isolated populations on Laysan Island, Midway Atoll, and Kure Atoll, which have *c.* 200, 300 and 30 potentially breeding pairs, respectively. Because survival can vary by year and population status, we studied the survival of cohorts over longer time series to provide a better understanding of changes in population survival between islands, during (reintroduction) population establishment, and with the emergence of new population threats such as avian botulism. Our objectives were to provide new estimates of total number for the nascent reintroduced population at Kure Atoll, annual survival estimates (using long-term data) for the birds on Laysan and Midway, and to summarise data on mortality from carcasses collected across the species' range. We report these data so that population risks and management actions can be better utilised for each of these separate, endangered populations.

Methods

Study areas

Laysan Island (25°46'N, 171°44'W; 413.6 ha), Midway Atoll (28°12'N, 177°22'W;

595.7 ha) and Kure Atoll (28°24’N, 178°18’W; where the only land of significant size, Green Island, covers 90.1 ha; Reynolds *et al.* 2012b) are small remote atolls in the northwest of the Hawaiian archipelago (Fig. 1) and form part of the Papahānaumokuākea Marine National Monument.

Laysan Island is unique in that it has the largest natural lake in the Hawaiian archipelago. This interior lake is hypersaline with seasonally expansive mudflats dominated by Brine Shrimp *Artemia franciscana* and Brine Flies *Neoscatella sexnotata* (Butler & Usinger 1963). Laysan Island’s terrestrial mean elevation (excluding the lake zone) is 4.3 m, vegetation is dominated by native shrubs and grasses and is described in Reynolds *et al.* (2012a). Midway Atoll is comprised of three islands: Sand, Spit and Eastern Islands, with mean elevations of 2.5 m, 0.8 m and 2.1 m, respectively, and their nature is described in Reynolds *et al.* (2017a). Kure Atoll is *c.* 2,400 km northwest of Honolulu and is the northernmost coral atoll in the world. It is comprised of two ephemeral sand spits and one stable island, Green Island (mean elevation of 2.8 m; Reynolds *et al.* 2012a), which has a substantial dune structure primarily

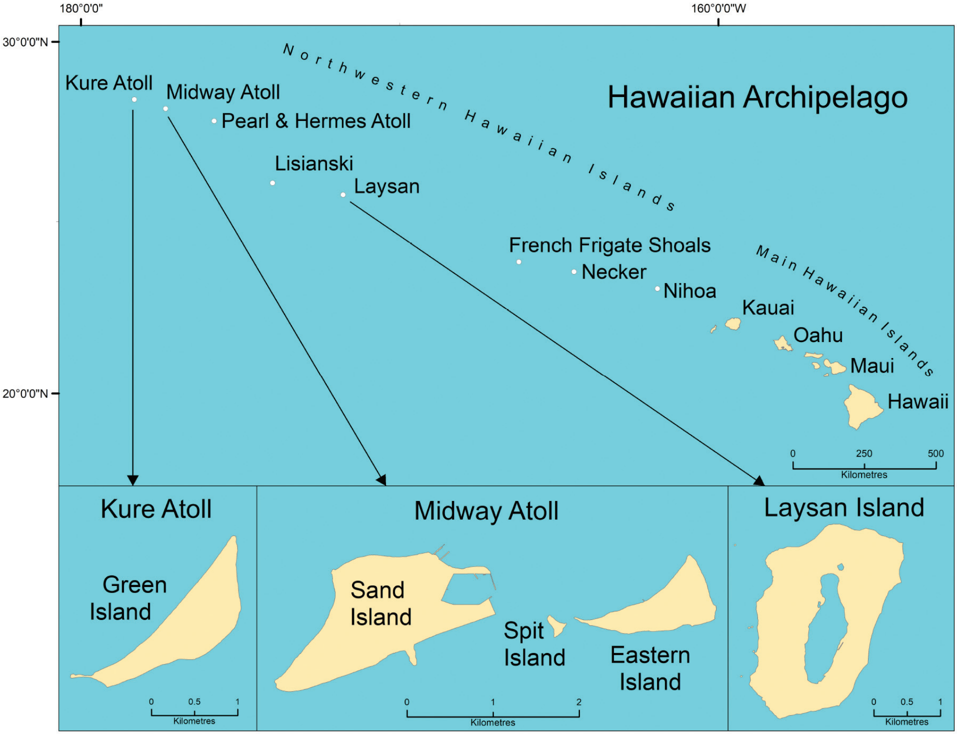


Figure 1. Map of islands in the Hawaiian archipelago, showing Laysan Island, Midway Atoll and Kure Atoll study areas.

composed of the succulent shrub Beach Naupaka *Scaevola taccada*, native grasses and vines, providing wildlife habitat and some protection from storm events and tsunamis. Habitat enhancements prior to the translocation of Laysan Teal included restoration of native vegetation, creating two ground water seeps, installing four rainwater catchment "guzzlers", and control of the invasive Big-headed Ant *Pheidole megacephala* to increase native plant arthropod biodiversity and abundance (C. Vanderlip, pers. obs.; PNMN 2014).

Population monitoring

Laysan Island and Midway Atoll populations of Laysan Teal have been marked and monitored for ≥ 15 and ≤ 10 years, respectively, and the third population recently translocated to Kure Atoll has been monitored for 4 years (51 months). Laysan Island birds were trapped, ringed and released during multiple periods from March 1998–August 2009 (Table 1). Bi-monthly surveys and opportunistic resightings to identify individuals from their rings were collected during June 1998–August 2014 (Table 1).

At Midway Atoll, the birds were captured, ringed, and released during multiple periods from May 2005–December 2015 (Table 1). Ducks were marked with a numbered USGS aluminium ring on one leg and with a plastic colour ring engraved with a unique code (Haggie Engraving, Crumpton, Maryland) or a field-readable engraved aluminium ring (Gey Band and Tag Company, Norristown, Pennsylvania) on the other leg. A subset of all ducks on Laysan Island and Midway Atoll were radio tracked for parts of this study (Reynolds 2004; Reynolds *et al.* 2008, 2013a). Cohorts included all birds captured within a calendar year and included hatch-year (HY) juveniles and adults.

The population at Kure Atoll was founded by 28 post-fledgling (juvenile) birds translocated from Midway Atoll on 3 September 2014 (PMNM 2014), but a planned second translocation has not yet been implemented. Candidates for translocation were captured during 31 August–2 September 2014 and each was marked with a unique ring combination as described above. Birds selected as founders met body condition requirements (including keel scores of ≥ 1) and were given a single vaccination for botulism (Botumink™), treated for internal parasites (ivermectin), and held in captivity on Midway then during transport for 22–56 h. Biosecurity included freezing of transport cages, quarantine, a holding period on Midway to pass seeds from the gastrointestinal tract, bathing of feet, and a cage change between transport from Midway and release on Kure Atoll. Birds were offered duck (feed) crumbles with mealworms and were gavaged (tube-fed) a high protein slurry at initial capture on Midway and before release at Kure. The Kure founder cohort was released on the day of arrival at water sources before sunset. Supplemental food was offered post-release from 4 September–7 December 2014. Video and photographs were taken by cameras installed at a water source in 2014 to identify uniquely marked individuals (GoPro HERO3™). Most observations were collected at least 1–3 times a week. Resighting of founder birds was conducted opportunistically and incidental to

Table 1. Laysan Teal capture, ringing and resighting effort at Laysan Island, Midway Atoll and Kure Atoll. Radio-tracking and resighting methods and effort are detailed in Reynolds (2004), Reynolds & Citta (2007) Reynolds *et al.* (2011, 2015, 2017a).

Location	Time periods of capture & ringing	Time periods of resighting & radio-telemetry effort
Laysan Island	*1998–2009* March–May 1998 October 1998–March 1999 May–June 1999 March–July 2000 August 2001 April–September 2004 April–September 2005 March–May 2007 August 2009	*1998–2014* June 1998–May 1999, August 1999–October 2012, April 2013–September 2013 and July 2014–August 2014: standardised mark-resight surveys & opportunistic resighting March–May 1998, October 1998–March 1999, May–June 1999, March–July 2000, October 2004 and October 2005: radio-telemetry
Midway Atoll	*2004–2015* October 2004 & October 2005: n = 20 and n = 22, respectively, ringed, post-fledgling birds translocated from Laysan Island and released May–December 2005 June 2006–February 2007 June–November 2007 August–November 2008 March–October 2009 October 2011 September–October 2013 August 2014 July–December 2015	*2004–2016* 2004–2007: resighting and radio-telemetry October 2007: mark-resight survey September 2008–January 2010, June 2010–November 2012 and November 2010–March 2016: bi-monthly standardised mark-resight surveys & opportunistic resighting
Kure Atoll	*2014* September 2014: n = 28 ringed, post-fledgling birds translocated from Midway Atoll and released	*2014–2018* September 2014–December 2018: opportunistic resighting incidental to management and ecological restoration activities January 2019–January 2020: opportunistic resightings – not used in the model

management and ecological restoration activities from September 2014 to December 2018. The sex, age, ring ID, time, location and brood status were recorded for individual birds sighted during this period.

Statistical analyses

We estimated the survival of the individually marked birds using the non-parametric Kaplan-Meier method (Pollock *et al.* 1989). As is common with small populations on remote islands, the long-term data collected did not meet the assumptions of a typical capture-recapture model framework (*e.g.* the Cormack-Jolly-Seber model, Williams *et al.* 2001) because of opportunistic ringing and sporadic resighting. An advantage of the non-parametric Kaplan-Meier method is that new individuals can be added to the sample at any time, thus maximising the sample sizes per cohort, and recorded deaths are included throughout the study. Encounter histories from uniquely-marked individuals collected from captures, systematic surveys, radio tracking, incidental resightings and collected carcasses therefore were applied to determine the last date an individual bird was observed alive, and to calculate its lifetime median resighting interval (*i.e.* the 50th percentile of intervals between resightings; see Reynolds *et al.* 2011, 2015, 2017a). Each bird's median resighting interval was used to approximate the date of death for a missing bird (details below). As the species does not migrate or disperse from the islands, uncertainty attributable to emigration is effectively absent in our study.

We applied the Kaplan-Meier survival curve estimation in Proc Lifetest in SAS v. 9.4 (SAS Institute Inc. 2012) to display results. For the purposes of this study, the end date for survival data collection was 31 Dec 2014 for Laysan Island, 7 Mar 2016 for Midway Atoll, and 20 Dec 2018 for Kure Atoll. To test for the effects of covariates on survival for the Laysan and Midway populations, we used log-rank tests in Proc Lifereg, also in SAS v. 9.4 (SAS Institute Inc. 2012). Initially, analyses of the Laysan and Midway cohorts were run separately, with the full model for each island including cohort, sex and their interaction terms. Chi-square tests were performed to determine the significance of each term, and the final reduced model for each island was determined by dropping insignificant terms and inspection of AICc values (Williams *et al.* 2001). Then we combined data from Laysan and Midway to investigate the effects of cohort, sex and island and their interactions, on survival. To estimate annual survival, we calculated the xth root of the survival rate at year x, and we calculated standard errors using the delta method. The delta method is based on a Taylor series expansion, used for calculating the variance of a function of normal random variables with known variance (Sokal & Rohlf 1981).

Carcasses of ringed birds were collected on being encountered in the field (USFWS & State of Hawai'i Division of Forestry and Wildlife data). A subset of carcasses was frozen, then sent to the USGS National Wildlife Health Center, Honolulu Field Station for necropsy to determine the cause of death. A subset of those samples was also submitted to the USGS National Wildlife Health Center for their standard mouse cross protection test. The test is based on an intraperitoneal injection of duck blood diluted in phosphate buffer into laboratory mice. If the sample contains toxin, the mice develop typical signs of botulism within a day following injection (Lindstom & Korkeala 2006).

Results

Survival

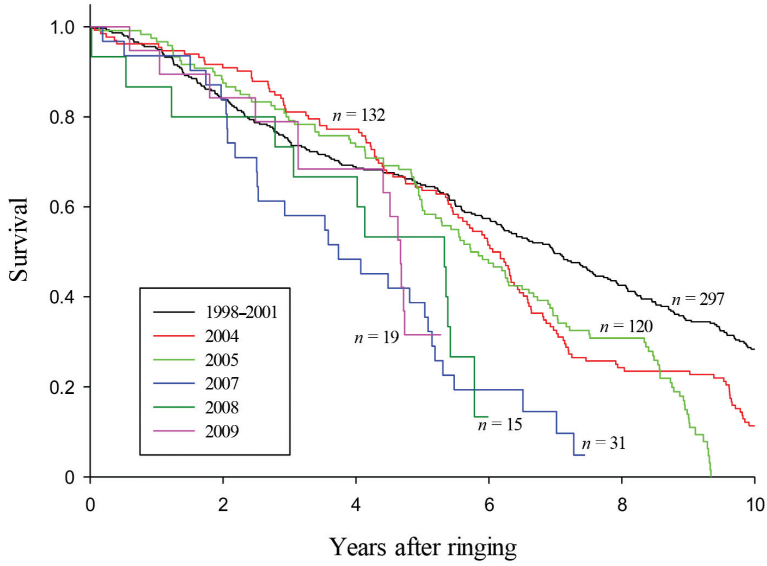
A total of 661 Laysan Teal (373 females, 274 males, and 14 juveniles of unknown sex) were caught and ringed on Laysan Island during 1998–2009. Juveniles of unknown sex were not used in any of our analyses. On omitting birds still alive at the end of the study, data for 614 birds (359 females, 255 males) from Laysan Island were analysed, derived from > 36,000 observations of ringed birds collected at Laysan Island through to September 2015. At Midway Atoll, between 2006–2011 we trapped and ringed individuals from the original 2004–2005 founder groups, and also the F_1–F_6 generations (*n* = 625 in total: 284 females, 302 males, and 39 juveniles of unknown sex). Again omitting individuals alive at the end of the study, data for 508 birds (252 females, 256 males) from Midway were used in our analyses, with > 24,000 resightings of these birds recorded at Midway Atoll through to May 2016. On Laysan Island, the longevity record was for a female first ringed at least a year after hatching in 1995 and was then recaptured in 1998 who was monitored for 14.29 years and therefore, reached > 15 years of age. On Midway, the longevity record was from a female ringed during her hatch-year in 2005 and subsequently monitored for > 10.29 years.

The annual survival estimates calculated for Laysan Teal over *x* years for *x* = 2–10, are illustrated in Table 2. On Laysan Island, survival rates (*n* = 614) averaged 0.86 (s.e. ± 0.06–0.12) over the 10 cohorts marked during 1998–2009, whilst annual survival at Midway (*n* = 508) averaged 0.76 (s.e. ± 0.08–0.02) over the seven cohorts marked during 2004–2011 (Table 2). Annual survival was higher on Laysan than Midway in all cohorts except 2007 (a La Niña drought year, https://www.pmel.noaa.gov/elnino/lanina-faq). Survival curves for the Laysan Island and Midway Atoll cohorts are shown in Fig. 2 and differences between islands and sexes are portrayed in Fig. 3 (averaged over cohorts). AICc values from log-rank tests for each island indicated that the best model included cohort and sex as the main effects, but without interaction terms (Laysan: AICc = 1317.29 for full model with interaction, AICc = 1311.69 for the reduced model with main effects; Midway: AICc = 1374.91 for full model, AICc = 1365.55 for reduced model). Similarly, when both islands were combined, the best model was a reduced model which included cohort, sex and island as the main predictor variables (AICc = 2726.10 for full model with all interactions, AICc = 2704.22 for reduced model with main effects but no interactions). *P* values and survival parameter estimates for the three reduced models are shown in Tables 3 & 4. Survival differed significantly across cohorts, between sexes and also between islands in all of the models (Table 3). Males had higher survival than females, and Laysan Island had higher survival than Midway Atoll, on average (Table 4).

Table 2. Estimation of annual survival for Laysan Teal by cohort (*i.e.* year of ringing) for each of the three populations: Laysan Island, Midway Atoll and Kure Atoll, Hawai‘i. Males and females are pooled together in this analysis. The average annual survival is given by the *x*th root of the survival estimated by Kaplan-Meier (KM) over *x* years, *x* = 2–10, from the Kaplan-Meier curve for each cohort (see Fig. 2). The number of years (*x*), over which annual survival was estimated, was determined by the number of years of data available for each cohort from time of ringing until the end of the study, except for the 1998–2001 cohort, which was truncated to 10 years of data to make it more comparable in length of time to the other cohorts. The standard error (s.e.) of annual survival was calculated using the delta method (Sokal & Rohlf 1981).

Cohort	Year *x*	K-M survival at year *x*	Annual survival (± s.e.) over *x* years
Laysan Island			
1998	10	0.353	0.901 (0.064)
1999	10	0.243	0.868 (0.063)
2000	10	0.302	0.887 (0.072)
2001	10	0.259	0.874 (0.086)
1998–2001	10	0.286	0.882 (0.048)
2004	9	0.235	0.851 (0.060)
2005	8	0.308	0.863 (0.068)
2007	6	0.194	0.761 (0.097)
2008	5	0.533	0.882 (0.153)
2009	4	0.684	0.910 (0.158)
Midway Atoll			
2004	8	0.150	0.789 (0.090)
2005	8	0.121	0.768 (0.075)
2006	7	0.154	0.765 (0.075)
2007	6	0.227	0.781 (0.084)
2008	5	0.250	0.758 (0.089)
2009	4	0.284	0.730 (0.080)
2011	2	0.537	0.733 (0.161)
Kure Atoll			
2014	4	0.333	0.760 (0.150)

a) Laysan Island



b) Midway Atoll

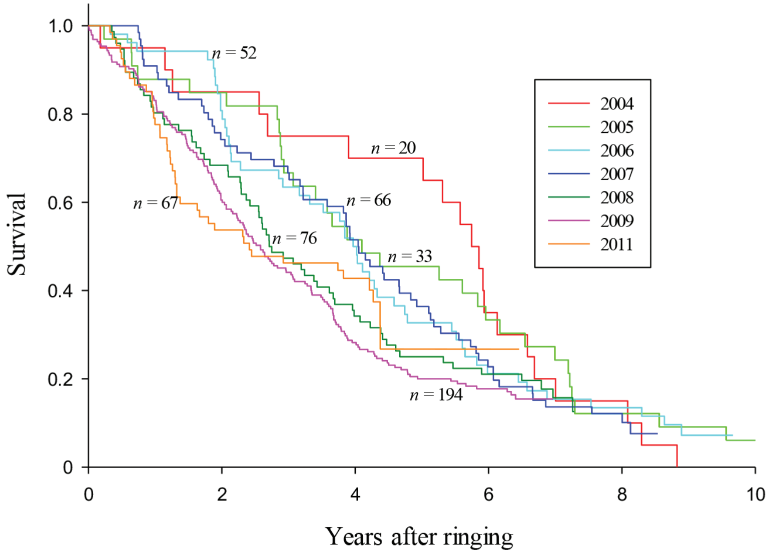


Figure 2. Laysan Teal survival estimates, determined by the Kaplan-Meier method, for different cohorts (*i.e.* year of ringing) on: a) Laysan Island and b) Midway Atoll, Hawai'i. Data are pooled over sexes in this analysis.

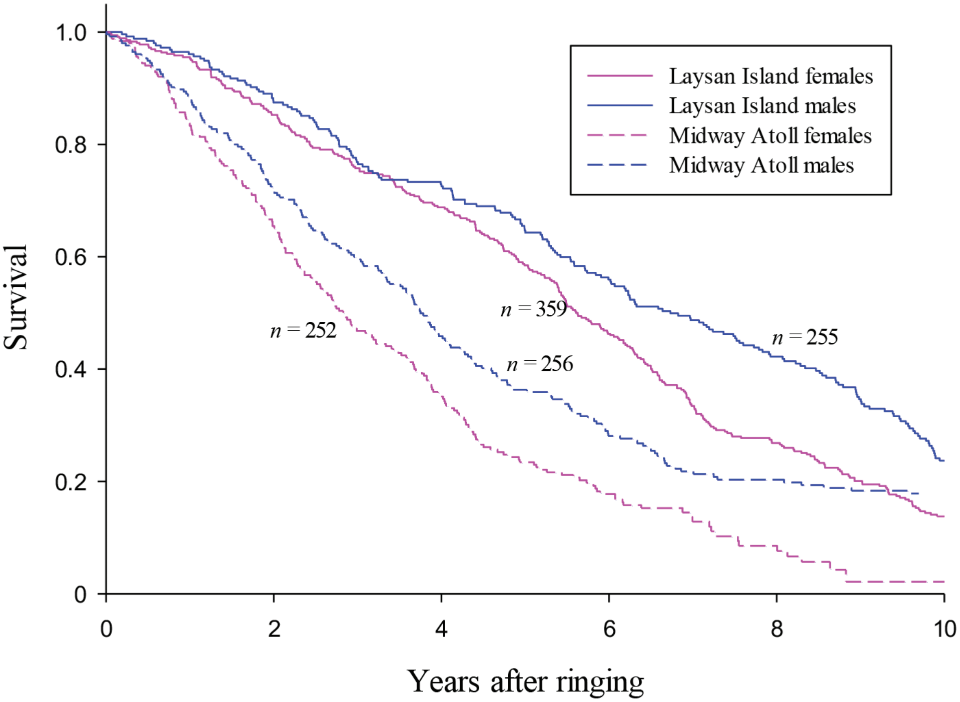


Figure 3. Laysan Teal survival estimates, determined by the Kaplan-Meier method, in relation to sex and island for Laysan Island (1998–2009) and Midway Atoll (2004–2011), Hawai'i. Data are grouped over cohorts for this analysis. Survival was found to be lower on Midway Atoll, and survival was lower for females than for males on both atolls. In particular, female survival was 40% lower on Midway Atoll than Laysan Island 5 years after ringing.

At Kure Atoll, > 2,729 resightings of the 28 founder cohort (all ringed) were collected between their initial ringing (31 August–2 September 2014) and December 2018. Median resighting intervals (MRI) varied from 3–31 days. Survival was 1.0 (*n* = 28) until March 2016. Over the four years to 2018, average annual survival was 0.76 (s.e. = 0.15), but the Kaplan-Meier estimates show that the survival of the founders dropped by 39% after 1.6 years, and then by another 41% at 2.5–3 years following two consecutive botulism outbreaks, respectively, yielding a survival of 0.36 for individuals three years after ringing (Fig. 4). Ten of 28 founders persisted in 2020 and survey counts indicate a population size of 60–70 birds (Andrew Sullivan-Haskins, pers. comm., Hawai'i Division of Forestry and Wildlife).

Mortality

Seventy-seven ringed Laysan Teal were recovered on Laysan Island (June 1998–May 2013), and 24 of the carcasses were sent to the USGS National Wildlife Health Center for necropsy. None tested positively for avian botulism. On Midway Atoll, 158 ringed carcasses were collected (December

Table 3. Results of log-rank tests comparing survival among cohorts, sex and island, for Laysan Teal on Laysan Island ($n = 614$) and Midway Atoll ($n = 508$), in Hawai'i. Interaction terms were not significant ($P > 0.05$) in any of the models.

	Wald chi-squared	**d.f.**	***P* value**
Laysan Island			
Cohort	34.19	5	< 0.0001
Sex	6.85	1	0.0089
Midway Atoll			
Cohort	14.32	6	0.0262
Sex	6.97	1	0.0083
Combined analysis			
Cohort	38.54	7	< 0.0001
Sex	13.79	1	0.0002
Island	5.54	1	0.0185

2004–July 2016), 53 were submitted for necropsy of which 70% were diagnosed with avian botulism (type C), and 100% of 23 ringed carcasses sent for the mouse cross protection test were positive for botulism (USGS-NWHC 2016). At Kure Atoll, 10 ringed carcasses were recovered (March 2016–May 2017). Four birds died while being treated for typical avian botulism symptoms including flaccid paralysis and six carcasses were sent for necropsy. All carcasses from Kure Atoll submitted for necropsy were diagnosed with avian botulism, as were all three tested via the mouse cross protection test (USGS-NWHC 2017).

Discussion

Our study is the first to estimate the survival for Laysan Teal using long-term data from each isolated population to provide improved vital rates for the species across its global range. We quantified variability in survival estimates for the annual cohorts and sexes with utility to improve estimates of extinction risks across the species range. For instance, the estimates can now be included as parameters in population viability analyses for each of the three populations. We compiled the mortality records for ringed birds and described avian botulism as an influential driver of differences in survival between the populations, specifically after 2008 on Midway Atoll, and after 2016 on Kure Atoll. Overall, annual survival was higher on Laysan Island where avian botulism outbreaks have not been documented, in contrast to Midway and Kure Atolls where avian botulism outbreaks are chronic.

Table 4. Parameter estimates from log-rank analysis comparing survival among cohorts, sex and island, for Laysan Teal on Laysan Island ($n = 614$) and Midway Atoll ($n = 508$), Hawai‘i. The interaction terms were not significant ($P > 0.05$) in any of the models, as such no interaction terms were included in any of these models and the main-effects estimates were used to make inference. A more negative parameter estimate implies lower survival relative to other levels of a factor (cohort and sex). Similarly, a more positive parameter estimate implies better survival. Estimates with zero degrees of freedom were not estimated because one level of each factor is set to zero and the other levels are compared relative to that one. Thus, the estimate with zero degrees of freedom is included in the intercept term and is the cohort with the best (or worst) survival; others have lower (or higher) survival relative to this one, depending on whether the estimates are more negative (or more positive), respectively. All three models indicate survival was better on Laysan Island than Midway Atoll, survival was lower for females in both populations, and cohorts had lower survival the closer in time to the year 2011 (*i.e.* the tsunami year).

Location	d.f.	Parameter estimate (± s.e.)
Laysan Island		
Intercept	1	2.098 (0.041)
1998–2001	0	0.000 (–)
2004	1	–0.099 (0.059)
2005	1	–0.153 (0.061)
2007	1	–0.485 (0.108)
2008	1	–0.442 (0.161)
2009	1	–0.425 (0.149)
Male	0	0.000 (–)
Female	1	–0.122 (0.047)
Midway Atoll		
Intercept	1	1.414 (0.118)
2011	0	0.000 (–)
2004	1	0.321 (0.203)
2005	1	0.340 (0.176)
2006	1	0.264 (0.157)
2007	1	0.253 (0.150)
2008	1	0.094 (0.147)
2009	1	–0.017 (0.128)
Male	0	0.000 (–)
Female	1	–0.193 (0.073)

Table 4 (*continued*).

Location	d.f.	Parameter estimate (± s.e.)
Combined Analysis		
Intercept	1	1.915 (0.082)
1998–2001	0	0.000 (–)
2004	1	–0.091 (0.066)
2005	1	–0.140 (0.067)
2006	1	–0.236 (0.122)
2007	1	–0.312 (0.094)
2008	1	–0.406 (0.101)
2009	1	–0.502 (0.088)
2011	1	–0.529 (0.125)
Male	0	0.000 (–)
Female	1	–0.152 (0.041)
Midway Atoll	0	0.000 (–)
Laysan Island	1	0.167 (0.071)

Hawai‘i's endangered waterbirds have experienced epizootics caused by ingestion of prey that has accumulated a neurotoxin produced by the bacterium *Clostridium botulinum* (avian botulism type C) in other ecosystems with high densities of bird carcasses (*e.g.* Hanalei National Wildlife Refuge, Hawai‘i; Reynolds *et al.* in press). Waterbird carcasses, carcass-feeding flies and their larvae initiate and spread avian botulism under specific environmental conditions where the dormant spores can germinate and grow rapidly. Each new carcass has the potential to develop toxin-accumulating necrophagous invertebrate vectors amplifying the outbreak (Wobeser 1997). Early seasonal surveillance and carcass removal before active and advanced carcass decay (*c.* three days post-mortem) is an effective mitigation strategy for preventing avian intoxication and reducing toxin concentration in necrophagous and secondary food webs (Anza *et al.* 2014; Evelsizer *et al.* 2010; Reed & Rocke 1992). Mitigation that could improve survival in the face of avian botulism includes vaccination and booster vaccination of females or a proportion of the populations (Rocke *et al.* 2000; Arimitsu *et al.* 2004). The two vaccinations cost less than US$0.5 per bird. Preventative surveillance and carcass removal with the aid of trained detector canines to locate carcasses of Hawaiian Duck *Anas wyvilliana* (or koloa maoli) has shown promise of improving carcass detection probability at Hanalei National Wildlife Refuge on Kaua‘i Island (Reynolds *et al.* in press).

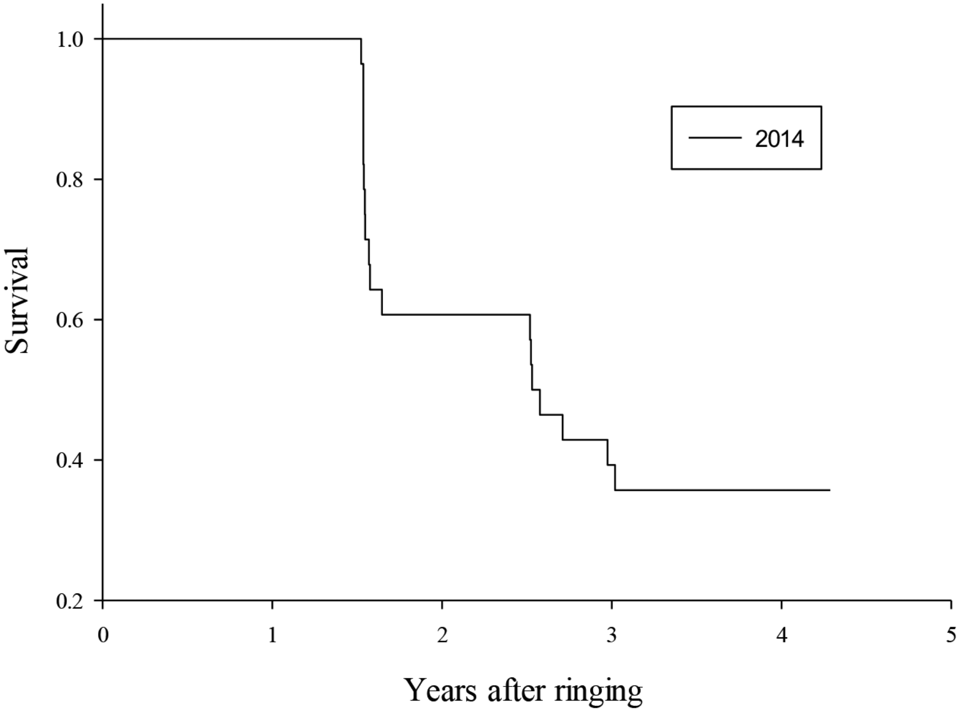


Figure 4. Survival by Kaplan-Meier estimation for 28 founder Laysan Teal translocated to Kure Atoll, Hawai'i, in 2014, of which 18 recovered individuals were included on determining survival rates up to the end of the study period (20 December 2018), with the other 10 birds still alive in January 2020 (Andrew Sullivan-Haskins, pers. comm., Hawai'i Division of Forestry and Wildlife data). Subsequent generations at Kure have not been ringed, so only the founder cohort was followed in this analysis.

Females were shown to have significantly lower survival than males in our long-term data sets. In previous short-term studies of Laysan Teal, with survival estimated over 1–3 year intervals, we did not detect these differences (Reynolds & Citta 2007; Reynolds *et al.* 2008, 2012a). Importantly, mortality of adult females has a disproportionately negative impact in Laysan Teal populations, in part because the females incubate the eggs and raise the ducklings without bi-parental care (although mate guarding of females by males may occur with their broods; M.H. Reynolds, pers. obs.). Additive mortality of the more vulnerable adult females may increase risk of demographic stochasticity in populations; thus, it is an important factor to consider on evaluating management actions for each population across the species' range (USFWS 2019). Increasing the range and number of Laysan Teal populations with the successful translocation techniques established for reintroduction of wild juvenile birds is expected to increase the probability of persistence and reduce the effect of the demographic stochasticity inherent in isolated small island populations (Akçakaya *et al.* 2004; USFWS 2009).

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Photograph: Laysan Teal at Midway Atoll, by Michelle Reynolds.