# **RESEARCH ARTICLE**

# Avian botulism is a primary, year-round threat to adult survival in the endangered Hawaiian Duck on Kaua'i, Hawai'i, USA

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## ABSTRACT

Adult survival is the most important demographic parameter influencing population dynamics for many bird taxa. Thus, understanding how survival probabilities and causes of mortality vary throughout the annual cycle is critical for developing informed and effective management strategies. In this study, we used radio-telemetry data to evaluate the effects of biotic (e.g., sex, peak [September–April] vs. off-peak [May–August] nesting seasons) and abiotic factors (e.g., rainfall, year, bi-monthly interval) on adult survival, estimate annual survival probabilities, and identify primary sources of mortality for Hawaiian Ducks (Anas wyvilliana), an endangered, non-migratory dabbling duck, on the island of Kaua'i, Hawai'i, USA over 2013 and 2014. Additionally, we used contemporaneous Hawaiian Duck carcass recovery and surveillance data to examine temporal and climatic associations with avian botulism outbreaks. Our results suggested bi-monthly survival decreased with total rainfall during the preceding 2-month interval. Survival did not vary with sex, between peak and off-peak nesting seasons, or between the two years of this study. Annual survival probabilities (62–80%) were relatively low compared to the closely related Laysan Duck (Anas laysanensis) on Laysan Island. Primary causes of mortality included avian botulism and presumed predation by cats (Felis catus). The botulism surveillance dataset revealed support for the effect of rainfall on the number of sick and dead birds recovered (n = 216), with generally a greater number of recoveries during months with middle-range total rainfall during the concurrent and preceding months. Our study provides critical baseline demographic data for population monitoring and highlights the importance of managing botulism risk and non-native mammalian predators for the recovery of the endangered Hawaiian Duck.

Keywords: Anas wyvilliana, avian botulism, Hawaiian Duck, Kaua'i, koloa maoli, mortality, radio-telemetry, survival

# LAY SUMMARY

- Understanding how adult survival probabilities and causes of mortality vary throughout the annual cycle is instrumental for developing informed and effective conservation strategies.
- We used radio-telemetry data to evaluate factors influencing adult survival and identify sources of mortality for the endangered Hawaiian Duck on Kaua'i, and we used botulism surveillance data to assess factors associated with avian botulism outbreaks.
- Avian botulism was the primary cause of adult mortality and posed a risk year-round.
- Increased rainfall was associated with lower survival and higher numbers of sick and dead birds attributed to botulism except during wettest periods when botulism recoveries decreased.
- Survival did not differ between sexes or peak and off-peak nesting seasons, but the rate of predation was higher for females, and all female predation events (n = 4) occurred during the peak-nesting season.
- Our study provides critical demographic data for population monitoring and highlights the importance of managing botulism risk and non-native mammalian predators (e.g., feral cats) for Hawaiian Duck recovery.

## Las precipitaciones se asocian con la supervivencia de adultos y el riesgo de botulismo aviar en la especie en peligro de extinción *Anas wyvilliana* en Kaua'i, Hawái, EEUU

### RESUMEN

La supervivencia de los adultos es el parámetro demográfico más importante que influye la dinámica poblacional de muchos taxones de aves. Por lo tanto, comprender cómo varían las probabilidades de supervivencia y las causas de mortalidad a lo largo del ciclo anual es fundamental para desarrollar estrategias de manejo informadas y efectivas. En

este estudio, utilizamos datos de radio-telemetría para evaluar los efectos de factores bióticos (e.g., sexo, temporada de anidación alta [septiembre-abril] vs. baja [mayo-agosto]) y abióticos (e.g., lluvia, año, intervalo bimensual) sobre la supervivencia de los adultos, para estimar las probabilidades de supervivencia anual y para identificar las fuentes primarias de mortalidad de Anas wyvilliana, un pato no migratorio en peligro de extinción, en la isla de Kaua'i, Hawái, EEUU, durante 2013 y 2014. Adicionalmente, utilizamos datos contemporáneos de recuperación de cadáveres y de vigilancia de A. wyvilliana para examinar las asociaciones temporales y climáticas con los brotes de botulismo aviar. Nuestros resultados sugirieron que la supervivencia bimensual disminuyó con la precipitación total durante el intervalo de 2 meses precedente. La supervivencia no varió con el sexo, entre las temporadas de anidación altas y bajas, o entre los dos años de este estudio. Las probabilidades de supervivencia anual (62-80 %) fueron relativamente bajas en comparación con las de la especie estrechamente relacionado A. laysanensis en la isla de Laysan. Las principales causas de mortalidad incluyeron el botulismo aviar y la presunta depredación por gatos (Felis catus). El set de datos de vigilancia de botulismo apoyó el efecto de las precipitaciones sobre la cantidad de aves recuperadas enfermas y muertas (n = 216), con una mayor cantidad de recuperaciones generalmente durante los meses con precipitaciones totales de rango medio en los meses concurrentes y precedentes. Nuestro estudio proporciona datos demográficos de referencia críticos para el monitoreo poblacional y destaca la importancia de gestionar el riesgo de botulismo y los depredadores mamíferos no nativos para la recuperación de A. wyvilliana, una especie en peligro de extinción.

Palabras clave: Anas wyvilliana, botulismo aviar, Kaua'i, mortalidad, radio-telemetría, supervivencia

## INTRODUCTION

Accurate estimates of demographic parameters are critical for addressing theoretical and applied ecological questions as well as understanding and managing avian populations. For species of conservation concern, demographic data are particularly important for assessing population status, determining the underlying mechanisms limiting population recovery, predicting population response to proposed management actions, and consequently, developing informed and effective conservation strategies (Morris and Doak 2002; Norris 2004; Doak et al. 2015). However, such information is often unavailable for many rare and listed species, and applying information from closely related or surrogate species can be inappropriate (Caro and O'Doherty 1999; Morris and Doak 2002; Murphy et al. 2011).

The Hawaiian Duck (or koloa maoli, *Anas wyvilliana*) is a non-migratory dabbling duck and the only remaining endemic duck in the main Hawaiian Islands of more than 12 Anatids found in the fossil record (Olson and James 1982; Burney et al. 2001; Iwaniuk et al. 2009). Qualitative records suggest Hawaiian Ducks were once common throughout the Hawaiian Islands, but they experienced substantial population declines during the early 20th century (Banko 1987). Currently, they are primarily restricted to the islands of Kaua'i and Ni'ihau (Wells et al. 2019; Malachowski 2020). Despite being among the first species listed as federally endangered in 1967, recovery remains hindered by a scarcity of information on key demographic parameters and the factors that most influence those vital rates (USFWS 2011).

Similar to many other endemic island bird populations (Blackburn et al. 2004; Atkinson and LaPointe 2009; Fordham and Brook 2010), Hawaiian Duck population persistence on Kaua'i is thought to be threatened by pathogens, introduced predators, and habitat loss and alteration

(USFWS 2011; Malachowski et al. 2018). Suspected outbreaks of Type C avian botulism involving Hawaiian Ducks were reported as early as the 1950s and 1960s (Brock 1953; Swedberg 1967), with more regular reports beginning in the 1980s (Engilis Jr. et al. 2020; Reynolds et al. 2021). Avian botulism causes extensive seasonal mortality among migratory waterfowl at temperate and subarctic latitudes of North America (Wobeser 1997a; Rocke and Bollinger 2007). However, risk to Hawaiian Ducks might be amplified by year-round conditions (e.g., warm temperatures, nutrient rich wetland and flooded agricultural environments) conducive to the growth of Clostridium botulinum (i.e. the anaerobic bacteria that produces botulinum neurotoxins) and the perpetuation of the carcass-maggot cycle, a primary and rapid pathway for the proliferation of avian botulism, whereby waterbirds ingest toxin-laden fly larvae, die, and become substrate for additional toxigenesis and oviposition of necrophagous flies (Wobeser 1997b; Rocke and Bollinger 2007; Espelund and Klaveness 2014). Further, exposure may be increased given high concentrations of non-migratory birds on limited suitable wetlands. Introduced predators such as cats (Felis catus), dogs (Canis lupus familiaris), rats (Rattus spp.), and Barn Owls (Tyto alba) are thought to primarily target eggs and/or ducklings, and the relative risk to adult Hawaiian Ducks is unknown (USFWS 2011; Malachowski et al. 2018). Like other dabbling ducks, Hawaiian Ducks nest in upland areas and females perform all nest building and incubation (Malachowski et al. 2018); thus, females may be particularly vulnerable to terrestrial predators.

Adult survival is the most important demographic rate influencing population growth for many bird taxa (Sæther and Bakke 2000; Hoekman et al. 2002; Stahl and Oli 2006; Coluccy et al. 2008), and understanding how survival probabilities and causes of mortality vary throughout specific phases of the annual cycle is critical for Hawaiian Duck conservation and management (USFWS 2011). Currently, there are no survival estimates for the species, and the relative role of various mortality sources is unknown. Studies on the closely related, island endemic Laysan Duck (A. laysanensis) indicate adults have relatively high survival, particularly on Laysan Island-a small remote atoll in the Northwestern Hawaiian Islands lacking mammalian predators and botulism outbreaks (Reynolds and Citta 2007; Reynolds et al. 2008, 2020). For their continental congener, the Mallard (A. platyrhynchos; Lavretsky et al. 2015), studies suggest seasonal variation in survival is largely influenced by changes in predation risk (Dugger et al. 1994; Greenwood et al. 1995; Brasher et al. 2006; Fleskes et al. 2007). For example, female Mallards often experience high mortality during the breeding season because of predation at upland nesting sites (Brasher et al. 2006; Arnold et al. 2012). Such patterns may contribute to sex-specific variation in survival, which has implications for population structure (e.g., sex ratio) and effective population size (Johnson and Sargeant 1977; Brasher et al. 2006; Traill et al. 2010). Data from banding (2010–2015; C. P. Malachowski personal observation), counts (2010-2014; C. P. Malachowski personal observation), and carcass recoveries (2010-2019; K. J. Uyehara personal observation) of Hawaiian Ducks suggest a highly skewed sex ratio in favor of males on northern Kaua'i (>2:1), which could potentially be caused by lower adult survival in females than males.

In our study, we used radio-telemetry to track male and female Hawaiian Ducks to assess threats and evaluate the relative role of factors influencing adult survival and causespecific mortality. We studied birds year-round, as events in one season can affect demographic rates in subsequent seasons, and researchers have increasingly acknowledged the value of studying species throughout the full annual cycle (Myers 1981; Marra et al. 2015). Our primary objectives were to (1) evaluate the effects of biotic (e.g., sex, peak vs. off-peak nesting seasons) and abiotic (e.g., rainfall, year) factors on survival probabilities of adult Hawaiian Ducks over a 2-year period, (2) estimate bi-monthly and annual survival, and (3) determine if cause-specific mortality rates varied between sexes. We predicted that, similar to continental Anas, females would have lower annual survival than males because of increased predation during the breeding season (Brasher et al. 2006; Arnold et al. 2012). We further predicted a positive relationship between survival and rainfall associated with increased wetland resources (e.g., food, shelter from predators), except for exceptionally wet conditions (e.g., major flooding) which were expected to decrease survival. We also predicted avian botulism to be a significant source of mortality given the relatively substantial botulism outbreaks reported during the year preceding this study (K. J. Uyehara, USFWS, personal observation). Thus, our secondary objective was to examine how climatic variables were associated with avian botulism outbreaks. We predicted warmer air temperature and lower rainfall would lead both to improved conditions for

toxigenesis and the carcass-maggot cycle (Wobeser 1997a; Rocke et al. 1999; Rocke and Samuel 1999) and reduced wetland availability, thereby increasing concentrations of birds at risk to mortality from botulism.

# METHODS

# Study area

We conducted fieldwork during 2012-2014 on the island of Kaua'i, Hawai'i, USA. Kaua'i and the island of Ni'ihau, located 29 km to the southwest, support the only remaining non-hybridized population of Hawaiian Ducks (Wells et al. 2019; Malachowski 2020). Rainfall on Kaua'i is primarily orographic and varies substantially with altitude as persistent northeast trade winds force humid air masses over the mountains (MacDonald et al. 1960). Mean annual rainfall ranges from <50 cm yr<sup>-1</sup> on the leeward coast to 1,000 cm yr<sup>-1</sup> on Mount Wai'ale'ale (1,598 m elevation) in the island interior (Giambelluca et al. 2013). At lower elevations, precipitation generally varies seasonally with decreased rainfall during summer months. The predator community posing risk to adult ducks on Kaua'i includes feral and free-ranging cats, dogs, Barn Owls, and, potentially, feral pigs (Sus scrofa) and Hawaiian Short-eared Owls (Asio flammeus sandwichensis; USFWS 2011; Raine et al. 2020). Although the diet of both owl species is generally dominated by small mammals, they are known to prey on small- to medium-bodied birds in Hawai'i (Snetsinger et al. 1994; Mostello and Conant 2018; Raine et al. 2019; Robinson et al. 2020).

Trapping and tagging of Hawaiian Ducks was centered at Hanalei National Wildlife Refuge (NWR) on the north shore of Kaua'i (22.205°N, 159.475°W). The refuge is managed to provide habitat for endangered Hawaiian waterbirds and the Hawaiian Goose (Branta sandvicensis), and the Hanalei region is the most important area for Hawaiian Ducks on Kaua'i (Banko 1987; USFWS 2011; Malachowski 2020). The lower Hanalei River flows through the 371-ha refuge and water from the river is diverted to manage the two dominant wetland types that occur on the refugemanaged palustrine emergent wetlands and irrigated taro (Colocasia esculenta) lo'i (Malachowski and Dugger 2018). Taro, an important agricultural crop in Hawai'i, is cultivated in shallowly flooded lo'i, which are small leveed impoundments similar to rice paddies. Mean annual rainfall at Hanalei NWR is 205  $\pm$  46 (SD) cm yr<sup>-1</sup>, varying subtly between a wet season (November to April; 20 ± 2 cm month<sup>-1</sup>) and drier season (May to October;  $15 \pm 2$  cm month<sup>-1</sup>; NCDC 2017).

# **Radio-tagging and monitoring**

During 24 November–11 December 2012 and 29 November–19 December 2013, we captured Hawaiian Ducks using customized baited swim-in traps (Hunt and

Dahlka 1953; Dugger and Malachowski 2013). We banded each bird with a U.S. Geological Survey (USGS) metal leg band and a uniquely coded, field-readable, colored leg band (Haggie Engraving, Crumpton, MD, USA; Gustafson et al. 1997). We sexed and aged birds using plumage characteristics (A. E. Engilis Jr. et al. personal communication) and cloacal examination. We weighed birds using a spring scale ( $\pm$ 5 g), measured culmen length using a dial caliper ( $\pm$ 0.1 mm), and calculated a body condition index (BCI) as body mass/culmen length (Harder and Kirkpatrick 1996) as an indirect measure of physiological condition at time of capture.

We transported a sample of adult birds ( $n_{\text{female}} = 50$ ,  $n_{\text{male}} =$ 67) in separate kennels from their capture site to a centralized site where a trained and experienced veterinarian implanted anesthetized birds with intracoelomic VHF radio-transmitters (Korschgen et al. 1984, 1996). We did not radio-tag birds undergoing remigial molt, females that were gravid or had brood patches, or any bird whose sexspecific BCI was in the lower 10th percentile for the species based on data collected during previous trapping efforts ( $n_{\text{male}}$  = 455,  $n_{\text{female}}$  = 96; C. P. Malachowski, Oregon State University, personal observation). Given few captured birds met these conditions and the duration of tracking was relatively long (up to 22 months), we believe these sampling criteria did not introduce significant sampling bias. Transmitters (Model AI-2M, Holohil Systems, Carp, Ontario, Canada) were configured to have a percutaneous antenna, 18-month battery life, and a mortality switch that doubled the pulse rate after 12 hr of inactivity. Fully configured transmitters weighed 18.0 g and averaged  $2.6 \pm 0.2\%$  $(mean \pm SD)$  of bird body mass (Fair et al. 2010). Following surgery, birds were placed back in their individual kennels and allowed to recover for at least 60 min prior to being released at their capture site.

We monitored the location and status (i.e. alive or dead) of tagged birds from December 2012 through December 2014 using a truck-mounted, 4-element null-peak antenna system or handheld 3-element antenna. We supplemented ground-based tracking with periodic aerial tracking using helicopters to relocate birds in remote areas not easily accessible from the ground (e.g., upper river valleys). We attempted to locate females daily and males every 2–4 days until birds died, transmitters failed, or transmitters were extruded (Malachowski et al. 2020) until the end of our study. When we detected mortality signals or suspected mortality had occurred (e.g., lack of movement between subsequent locations, relatively weak signal given transmitter proximity), we attempted to locate the transmitter as quickly as possible to confirm the bird's status.

When Hawaiian Duck carcasses or remains were recovered, we classified the suspected cause of mortality as predation by mammal or bird, avian botulism, other pathogen, anthropogenic, or unknown using a combination of evidence at the mortality site, external examination of the carcass, and necropsy. Although cause of mortality may be due to more than a single factor, we assumed mammalian predation occurred in cases where feather vanes were sheared, bones were broken and chewed, and tooth marks were evident on bones and transmitter (Thirgood et al. 1998; Blomberg et al. 2013). We assumed avian predation occurred when body feathers were cleanly plucked, muscle tissue was clearly removed, and carcasses lacked tooth marks (Thirgood et al. 1998). Fresh carcasses were submitted to the USGS National Wildlife Heath Center (NWHC) Honolulu Field Office for necropsy to provide a more comprehensive assessment of cause of mortality and differentiate predator induced trauma and scavenging, when possible. Heart blood was tested for botulinum toxin type C using mouse cross protection (Quortrup and Sudheimer 1943) at the NWHC, Madison, Wisconsin. If direct botulism testing was not possible, we attributed death to avian botulism if (1) no visible lesions, signs of trauma, or other diseases were identified during necropsy; (2) multiple mortalities and/or sick birds with botulism symptoms (e.g., flaccid paralysis of the neck and limbs, immobilized nictitating membrane) were concentrated; and (3) botulinum toxin was detected in other birds in the vicinity using serum and mouse-bioassay. If carcasses were too degraded to determine cause of death, we classified the cause as unknown. We examined the wings of each carcass for evidence of remigial molt to determine if mortality occurred during the bird's flightless period.

If we found transmitters without a carcass or remains (e.g., feathers, bones), or if we detected mortality signals but could not locate the transmitter and carcass (e.g., transmitters on private property where landowners prohibited access), it was possible that the bird extruded and lost its implant (Malachowski et al. 2020). In these cases, we determined transmitter loss using evidence at the transmitter recovery site or subsequent recaptures, band resightings, and recoveries, as described in Malachowski et al. (2020).

#### **Botulism surveillance**

During our study, USFWS personnel conducted botulism surveillance at least once weekly and up to 3 times daily to recover sick birds and carcasses at Hanalei NWR (K. J. Uyehara, USFWS, personal observation). During surveys, observers walked or drove vehicles around the perimeters of wetland impoundments and taro lo'i while scanning for sick and dead birds. During botulism outbreaks (i.e.  $\geq 4$  sick/dead birds per week), observers walked transects within affected impoundments and lo'i. Sick birds and carcasses were also recovered incidentally while performing other tasks on the refuge. For each encounter, observers recorded the bird's status as: (1) live, but sick (bird weak enough to capture easily); (2) fresh carcass ( $\leq 24$  hr dead); (3) moderately decomposed; or (4) severely decomposed (predominantly bones and feathers). We presumed botulism intoxication in live birds exhibiting flaccid paralysis of the neck or limbs, immobilized nictitating membrane, discoordination, and slow escape response (Wobeser 1997a). For carcasses, we used criteria described in the previous section to diagnose cause of mortality as botulism.

# **Statistical analyses**

Known-fate survival analysis. We formatted survival data for radio-tagged birds into live-dead encounter histories including 12 2-month survival intervals. We left-censored data to allow staggered entry of birds into the marked population, and we right-censored data for birds that we could no longer monitor because transmitter batteries failed, birds extruded transmitters, or birds exited the study area (Pollock et al. 1989). For 13 birds, we detected mortality signals or found transmitters without carcasses, but we could not clearly differentiate mortality and transmitter extrusion. Survival data for these birds were similarly right-censored.

We used known-fate modeling with the logit-link function in program MARK (White and Burnham 1999) to estimate bi-monthly survival probabilities and investigate the influence of various covariates on survival. The knownfate model assumed (1) the process of capturing and radio-tagging did not affect survival, (2) the fates among individuals were independent, and (3) censoring was unrelated to mortality (White and Burnham 1999). Therefore, we censored data from the first 14 days following transmitter attachment when birds are most vulnerable to surgery-related mortality (Mulcahy and Esler 1999). We assumed censorship associated with birds exiting the study area, experiencing transmitter failure, or losing transmitters was random and independent of fate. However, rightcensoring the 13 birds for which we could not differentiate mortality and transmitter loss may violate the third assumption, and we address this issue below.

We constructed a priori models using 7 covariates hypothesized to influence adult survival, including sex, rainfall, and additional temporal factors. We assessed linear, logarithmic (i.e. pseudo-threshold), and quadratic effects of concurrent bi-monthly rainfall and rainfall in the preceding 2-month interval (hereafter "lagged rainfall"), as rainfall and associated effects on habitat and resources may not have an immediate effect on survival. To further explore short-term temporal patterns in survival, we evaluated effects of bi-month (i.e. bi-monthly intervals differ within years but constant across years), biological season (peak nesting vs. off-peak nesting), and year (2013 vs. 2014), as well as general time-specific effects (i.e. bi-monthly intervals differ within and across years). Malachowski et al. (2019) described peak-nesting season as the 9-month period spanning September through May;

however, because of the temporal structure of our analysis (i.e. 2-month intervals), we considered the peaknesting period as September–April and off-peak nesting as May–August.

We used Akaike's Information Criterion values corrected for small sample sizes (AIC<sub>2</sub>), differences between a given model's AIC and the AIC of the top-ranked model  $(\Delta AIC)$ , and AIC model weights (w) to assess the relative support for each model in the candidate model set (Burnham and Anderson 2002; Arnold 2010). We evaluated all covariates using single-variable models, as well as additive combinations of covariates receiving strong support as single-variable models ( $\Delta AIC_{c} < 2.0$ ). If sex or season received strong support as single-factor effects, we considered a sex × season interaction because we predicted females would have lower survival than males during the peak-nesting season and equal survival during the remainder of the year. We included an intercept-only model to evaluate the relative support of other candidate models. For competitive models ( $\Delta AIC_c < 2.0$ ), we determined the amount of evidence for each covariate by evaluating 95% confidence limits on model coefficients ( $\beta$ ). Estimates for model coefficients are presented on the link scale. We used the delta method to estimate variance and 95% confidence intervals for annual survival probabilities (Powell 2007). There is no goodness-of-fit test for known-fate models (Cooch and White 2021). We report the deviance as the difference in  $-2*\log(likelihood)$  of a given model and that of the saturated model, and this provides a measure of relative model fit.

Because right-censoring survival data for the 13 birds for which we could not clearly differentiate mortality and transmitter loss may violate the model assumption that censoring is unrelated to mortality, we conducted a separate known-fate analysis that accounted for uncertainty in bird fate to provide a conservative estimate of annual survival (Hupp et al. 2008; Mateo-Moriones et al. 2012; Davis et al. 2017). We modified encounter histories by assuming each of the 13 birds died, and we used the top model structure from the previous analysis to generate conservative estimates of annual survival probabilities.

**Cause-specific mortality rates.** We examined differences in cumulative cause-specific mortality rates between females and males using the non-parametric cumulative incidence function estimator (NPCIFE; Heisey and Patterson 2006) with the *csm* function (wild1 package; Sargeant 2011) in Program R (version 3.5.2, R Development Core Team 2018). The NPCIFE, a generalization of the Kaplan–Meier method, allows for staggered entry and right-censoring and appropriately estimates incidence by accounting for competing risks, rather than censoring them (Heisey and Patterson 2006). We used bi-monthly intervals, beginning 1 January following radiotagging and ending at time of mortality or last observation,

as time to event. We estimated annual cause-specific mortality (±95% confidence intervals) by pooling data across years. We were primarily interested in comparing hazards from the two factors of concern to management - predators and botulism. However, we included categories for anthropogenic causes and other pathogens to account for competing risks. We also included a category, "unknown," for cases when we could not assign mortalities to a specific source; therefore, rate estimates for known causes are considered conservative. In comparing sex-specific hazards from predators and botulism, we assumed birds dying from unknown causes occurred in similar proportions as known sources of mortality. To assess this assumption, we used two-sided Fisher's exact tests to test if the composition of sexes of birds with unknown causes of mortality differed from birds with identified causes of mortality. We conducted 3 separate tests comparing unknown causes to all known causes, only predation, and only botulism. Based on this analysis, the independent variable sex could not differentiate unknown from known mortalities (P > 0.05), suggesting birds dying from unknown causes were representative of other sources of mortality.

Botulism-climate analysis. We used generalized linear models (GLMs) to examine further the relationship between botulism and climate conditions using data collected during refuge botulism surveys and other refuge activities. The response variable was the monthly number of dead and sick Hawaiian Ducks for which the presumed cause of mortality or illness was botulism. We included sick birds because ingestion of the botulinum neurotoxin often leads to lethal paralysis, and intoxicated birds often die from drowning, respiratory failure, or dehydration. We therefore assumed they would have died without intervention and treatment. If sick birds were treated, released, re-intoxicated, and recovered again (n = 3), we censored their second recovery record to prevent double-sampling. Ducklings (n = 17) represented a relatively small proportion of recoveries and were removed from the sample. For sick birds and fresh carcasses (i.e. status 1 and 2), we assigned date of mortality as the date birds were found. For moderately decomposed carcasses (i.e. status 3), we backdated mortality date by 3 days from recovery date. We could not accurately estimate date of mortality for severely decomposed carcasses (i.e. status 4; n = 54), and they were removed from the sample. We further limited our sample to birds with estimated mortality dates spanning from January 2013 through December 2014 to align with the data collection period for the remainder of the study.

We accounted for temporal variation in search effort by including monthly botulism surveillance time (person hours), an index for effort, as a covariate in all models. Missing values for individual survey times (39%) were calculated as the mean survey time for a given location. If an individual (or individuals, for 2-person surveys) had  $\geq 2$  surveys with duration data for a given location, we used the observer-specific mean survey duration for that location. We calculated person hours for each survey as duration × number of observers, and summarized monthly surveillance data by calculating the total person hours for each month. We assumed monthly effort associated with activities during which incidental recoveries of sick and dead birds occurred (e.g., farming, management, other surveys) was constant throughout the study period (K. J. Uyehara, USFWS, personal observation).

Explanatory variables for botulism models included linear and logarithmic effects of mean daily maximum air temperature for each monthly interval. We also considered linear, logarithmic, and quadratic effects of concurrent, lagged, and concurrent-lagged monthly rainfall. Lagged rainfall was the total rainfall during the previous monthly interval, and concurrent-lagged rainfall was the total rainfall during the current and previous intervals combined. For all analyses, we obtained rainfall and temperature data from USGS climate station USC00518165 at Princeville Ranch, ~1 km north of the refuge (National Climate Data Center, https://www.ncdc.noaa.gov). Missing data (4% for rainfall, 8% for temperature) were supplemented with data from nearby climate stations (USC00513386, US1HIK10007, USC00514561).

Because initial Poisson regression analysis indicated overdispersed count data (i.e. variance > mean), we used a negative binomial error distribution and logarithmic link function to account for overdispersion (Zuur et al. 2009) using the glm.nb function (MASS package; Venables and Ripley 2002). Prior to model fitting, we used the Pearson correlation coefficient to evaluate the relatedness of continuous covariates and did not include strongly correlated variables (|r| > 0.6) in the same model. We evaluated each climate covariate as an additive combination with surveillance time and advanced covariates in models receiving strong support (<2 AIC<sub>2</sub>) to more parameterized models. We used a model including only surveillance time and a null model (i.e. intercept only) for comparison. All models included an overdispersion parameter. We used model selection procedures described above in the known-fate analysis to assess the relative support for each model in the candidate model set and determine the amount of evidence for each covariate in competitive models. We calculated Nagelkerke's pseudo- $R^2$  ( $R^2_N$ ; Nagelkerke 1991) for each model to provide a familiar index of goodness-of-fit.

## RESULTS

We radio-tagged 50 female ( $n_{2012} = 34$ ,  $n_{2013} = 16$ ) and 67 male ( $n_{2012} = 31$ ,  $n_{2013} = 36$ ) Hawaiian Ducks. One male died from botulism and 1 female from unknown causes within 14 days of transmitter attachment and were excluded from analyses. One male was recovered sick with

<b>TABLE 1.</b> Model selection results for a known-fate survival analysis for radio-tagged adult Hawaiian Ducks ( $n_{\text{female}} = 49$ , $n_{\text{male}} = 66$ )
on Kaua'i, Hawai'i, USA, 2013–2014. Covariates include sex, rainfall (total rainfall during concurrent 2-month interval), lagged rainfall
(total rainfall during previous interval), bi-month (i.e. bi-monthly intervals differ within years but constant across years), biological
season (peak nesting [September-April] vs. off-peak nesting [May-August]), year (2013 vs. 2014), and general time-specific effects (i.e.
bi-monthly intervals differ within and across years). Models are ranked from most to least supported based on Akaike's Information
Criterion adjusted for small sample sizes (AIC). Model diagnostics include $\Delta$ AIC, AIC, weights (w), number of parameters (k), and
model deviance.

Model	ΔAIC <sub>c</sub> <sup>a</sup>	<i>W</i> <sub>i</sub>	k	Deviance
log_(lagged rain)	0.00	0.308	2	15.65
Lagged rain	0.31	0.263	2	15.96
Lagged rain + lagged rain <sup>2</sup>	2.05	0.110	3	15.68
Null	2.70	0.080	1	20.37
Season	2.78	0.077	2	18.43
Year	3.49	0.054	2	19.15
log_(rain)	4.64	0.030	2	20.29
Rain	4.67	0.030	2	20.33
Sex	4.70	0.029	2	20.36
Rain + rain <sup>2</sup>	6.21	0.014	3	19.84
Bi-month	8.20	0.005	6	15.70
General time	12.33	0.001	12	7.35
<sup>a</sup> Lowest AIC <sub>2</sub> value = 190.19.				

botulism symptoms, treated for botulism, and released after 8 days of rehabilitation. Because the bird was found during non-tracking activities and treated in accordance with standard refuge protocol, we continued tracking the bird and retained post-release data in the survival analysis. We detected mortalities for 24 birds, including 20% of females and 21% of males. Birds were last detected with non-mortality signals a median of 1.5 days prior to mortality signals (n = 22;  $\bar{x} = 3.2 \pm 1.0$  days [mean  $\pm$  SE]; range: 0-17), and carcasses were found a median of 1 day after mortality signals were detected (n = 22;  $\bar{x} = 1.0 \pm 0.4$  day; range: 0-9). Two carcasses were found prior to activation of mortality sensors. We right-censored data for birds that extruded transmitters ( $n_{\text{female}} = 13$ ,  $n_{\text{male}} = 15$ ) or had signal loss ( $n_{\text{female}} = 14$ ,  $n_{\text{male}} = 16$ ) beginning with the interval immediately following the interval when last confirmed alive. For 13 birds ( $n_{\text{female}} = 6$ ,  $n_{\text{male}} = 7$ ), it was unclear if the bird died or extruded its tag. In these situations, we detected mortality signals towards deep water or dense vegetation, but could not locate the transmitter or carcass (n = 7), we detected mortality signals towards private property where we could not gain access (n = 4), or we recovered transmitters in a river, but could not locate the carcass (n = 2). Survival data for these birds were right-censored in the primary known-fate analysis but treated as mortality events when generating conservative annual survival estimates. Annual rainfall during 2013 (158 cm) and 2014 (180 cm) was 22% and 12% lower, respectively, than the long-term (1938–2012) average.

# **Survival probabilities**

Various functional forms of lagged rainfall were the only explanatory variables associated with survival probability in competitive models and garnered 68% cumulative model weight (Table 1). The most parsimonious model indicated bi-monthly survival probability decreased with lagged log-rainfall ( $\beta = -1.238$ , 95% CI: -2.367 to -0.109; Figure 1), and this model was 3.9 times more likely than the null model, which was the next best model that lacked a rainfall effect. Survival probability did not differ between males and females; the confidence interval for the beta estimate broadly overlapped zero ( $\beta_{sex} = 0.056$ , 95% CI: -0.776 to 0.889). Based on the top model, annual survival of Hawaiian Ducks was 79.6% (95% CI: 70.3–88.9) in 2013 and 70.0% (95% CI: 59.7–80.3) in 2014. Annual survival based on our conservative approach was 65% (95% CI: 55–76) for 2013 and 62% (95% CI: 52–73) for 2014.

# **Cause-specific mortality**

The most common cause of mortality for radio-tagged Hawaiian Ducks was avian botulism (33%), followed by predation (21%), anthropogenic causes (8%), and other pathogens (4%; Table 2). We could not determine cause of mortality for 33% of dead birds. All birds with mortality ultimately attributed to botulism tested positive. Predation accounted for 50% of mortalities for which the cause could be determined for females and only 13% of mortalities for males. All female predation events occurred during the peak-nesting season (Table 2). Birds were killed by mammalian ( $n_{\text{female}} = 3$ ,  $n_{\text{male}} = 1$ ) and avian ( $n_{\text{female}} = 1$ ) predators. Anthropogenic mortalities involved 2 males that were presumably entrapped and died in a deep water control box used for taro lo'i irrigation. In addition, 1 male died from multi-organ inflammation, which may have been caused by bacterial infection (T. M. Work, USGS National Wildlife Health Center, personal communication); the bird tested



FIGURE 1. Association between lagged rainfall (mm; bar graph) and bi-monthly survival probabilities of Hawaiian Ducks (with 95% confidence intervals; line graph) during January 2013 through December 2014 on northern Kaua'i, Hawai'i, USA.

**TABLE 2.** Number of radio-tagged adult Hawaiian Ducks with various causes of mortality during the peak nesting season (September–April) and off-peak nesting season (May–August) on Kaua'i, Hawai'i, USA, 2013–2014. The initial sample included 115 radio-tagged birds that survived the 2-week post-surgery censoring period ( $n_{\text{female}} = 49$ ;  $n_{\text{male}} = 66$ ).

Season				Mortality source			Tota
	Sex	Botulism	Predation	Anthropogenic	Other pathogens	Unknown	
Peak nesting	Female	4	4	0	0	1	ç
	Male	4	0	2	1	4	11
Off-peak nesting	Female	0	0	0	0	1	1
	Male	0	1	0	0	2	3

negative for botulism. None of the 24 carcasses exhibited evidence of remigial molt (i.e. all had fully emerged primary feathers).

Cause-specific mortality analysis suggested females experienced higher rates of annual predation compared to males (8% vs. 2%), but annual rates of mortality attributed to botulism were similar for males and females (Table 3). The cumulative risks of mortality due to anthropogenic cause and other pathogens were low for males (<3% each), and females did not experience mortality associated with these causes.

## **Botulism surveillance**

During 2013–2014, 216 carcasses and sick birds were recovered and met our criteria for botulism analysis; monthly recoveries ranged from 1 to 34 birds ( $\bar{x} = 9$ ; Figure 2). We recognize some uncertainty in assigning cause of mortality; however, 18 of the 19 birds (95%) both presumed to have died from botulism using field criteria and submitted for botulism testing were positive for botulinum toxin (summary excludes 2 birds with inconclusive test results).

We observed support for the effect of concurrent-lagged rainfall on the number of sick and dead birds recovered, with 3 of the top 4 models containing a concurrent-lagged rainfall effect and receiving 49% of model weight (Table 4). The top candidate model included a quadratic structure of concurrent-lagged rainfall and indicated the number of botulism-related mortalities was greater during months with middle-range concurrent-lagged rainfall totals (Figure 3;  $\beta_{rain} = 0.0306, 95\%$  CI: 0.0098 to 0.0516;  $\beta_{rain}^2 = -0.00004, 95\%$  CI: -0.00007 to -0.00001). The model was moderately well fit ( $R^2_N = 0.47$ ) and 6.5 AIC<sub>c</sub> lower than the null model.

## DISCUSSION

Our study provides the first assessment of factors influencing adult survival and cause-specific mortality in the endangered, island endemic Hawaiian Duck. Overall,

**TABLE 3.** Estimates of sex-specific mean annual mortality for adult Hawaiian Ducks on Kaua'i, Hawai'i, USA, 2013–2014. Estimates and 95% confidence intervals are provided for mortality associated with avian botulism, predation, anthropogenic, other pathogens, and unknown causes.

Cause of mortality	Female (95% Cl)	Male (95% CI)	
Botulism	0.098 (0-0.219)	0.077 (0–0.195)	
Predation	0.077 (0-0.157)	0.024 (0-0.089)	
Anthropogenic	_	0.028 (0-0.082)	
Other pathogens	_	0.014 (0-0.053)	
Unknown	0.075 (0-0.180)	0.130 (0-0.261)	



FIGURE 2. Number of botulism-related sick and dead Hawaiian Ducks recovered during refuge botulism surveillance and other activities between January 2013 and December 2014 at Hanalei National Wildlife Refuge, Kaua'i, Hawai'i, USA. Ducklings and severely decomposed carcasses are not included.

annual adult survival probability during 2013 and 2014 (62-80%) was high compared to closely related continental Anas such as Mallards and Mottled Ducks (~50-65%; Francis et al. 1998; Coluccy et al. 2008; Varner et al. 2014; Bielefeld et al. 2020; Drilling et al. 2020), but lower than its Hawaiian island congener, Laysan Ducks (~86% on Laysan Island; Reynolds 2002; Reynolds and Citta 2007; Reynolds et al. 2020). We provided alternate estimates for annual survival to account for cases where we could not directly differentiate bird mortality and transmitter loss; however, these conservative estimates (62-65%) are probably unrealistically low because many specific instances associated with uncertainty were more consistent with tag loss rather than mortality (Malachowski et al. 2020). Avian botulism was the principal cause of adult mortality and affected males and females at similar rates. Whereas we predicted increased botulism-related sickness and mortality during warmer, drier months (e.g., Wobeser 1997a; Rocke

and Samuel 1999; Rocke et al. 1999; Work et al. 2010), we found no support for a temperature effect. We did find support for a rainfall effect but with generally more recoveries during months with middle-range combined concurrent and lagged monthly total rainfall. Also contrary to our prediction, survival did not differ between sexes or seasons. However, females had higher mortality attributable to predators than males, and all predations of females (n = 4) occurred during the peak-nesting season. These results provide crucial demographic data for population monitoring and emphasize the importance of managing botulism risk and non-native mammalian predators, such as feral cats, for Hawaiian Duck recovery.

Avian botulism was the primary cause of adult mortality for Hawaiian Ducks and posed a risk throughout the year. Botulism was linked to half of all identified mortality events among radio-marked birds and to over 200 sick and dead ducks recovered during refuge surveys between

**TABLE 4.** Model selection results for a priori negative binomial regression models examining the effects of rainfall and temperature on the number of botulism-related sick and dead Hawaiian Ducks at Hanalei National Wildlife Refuge, Kaua'i, Hawai'i, USA, 2013–2014. Botulism surveillance time was used as an index for survey effort and included as a covariate in all models except the null model. All models include an intercept and overdispersion parameter. Models are ranked from most to least supported based on Akaike's Information Criterion adjusted for small sample sizes (AIC<sub>c</sub>). Model diagnostics include  $\Delta AIC_{c'} AIC_{c}$  weight ( $w_{j}$ ), number of parameters (k), model deviance, and Nagelkerke's pseudo- $R^2$  ( $R^2_{v}$ ).

Deviance	R <sup>2</sup> <sub>N</sub>
25.98	0.47
24.66	0.36
25.08	0.27
24.62	0.33
24.76	0.41
24.66	0.33
25.02	0.30
24.95	0.30
24.85	0.29
25.06	0.28
25.07	0.28
25.22	0.33
25.21	-
	25.21

2013 and 2014. Clostridium botulinum is a major disease agent for waterbirds worldwide; however, unlike outbreaks in temperate, or even subtropical (e.g., Midway Atoll), regions that are predominantly restricted to the summer and fall (Wobeser 1997a; Rocke and Bollinger 2007; Work et al. 2010), botulism is a year-round issue for Hawaiian Ducks and possibly linked to environmental conditions permitting toxin production and vector activity throughout the year, or the interaction of environmental conditions and carcass abundance in an ecosystem with a high density of resident birds and few vertebrate scavengers (Wobeser 1997b; Rocke and Bollinger 2007). Although there is less documentation of outbreaks in tropical climate zones compared to temperate zones (Espelund and Klaveness 2014), our findings suggest botulism can be a major source of mortality for non-migratory waterbirds in tropical regions where the disease occurs.

Contrary to our predictions, increased rainfall was associated with lower adult survival and generally with higher numbers of sick and dead birds attributable to botulism except during periods with highest rainfall when the numbers of botulism recoveries decreased. We anticipated a positive relationship between survival and rainfall following periods of low to moderate precipitation as rainfall would increase wetland resource availability. However, such an effect may have been buffered by year-round management of core wetland habitat on our study area (Malachowski and Dugger 2018) where resources are available even during relatively dry periods. Instead, it is possible that moderate to heavy rainfall events mobilized spores and created conditions favorable for botulinum toxin production and vector activity in subsequent weeks. Consistent with that explanation, the severity of botulism outbreaks peaked during months with middle-range concurrent-lagged rainfall. The decline in botulism recoveries during periods with exceptionally high rainfall and flooding is not fully understood, but may be associated with the flushing of toxins from the system and dispersal of birds from centers of botulism activity. Given botulism was the primary mortality factor during our study and continued to be an issue at Hanalei NWR following our study (>500 dead Hawaiian Ducks during 2015–2020; K. J. Uyehara, USFWS, personal observation), we suggest additional efforts are needed to understand the relationships between environmental variables, habitat management, farming practices, and botulism outbreaks on northern Kaua'i.

Although overall survival probabilities did not vary between sexes or seasons in our 2-year study, the rate of predation was over 3 times higher for females (0.077; n = 4) than males (0.024; n = 1), and all predations on females occurred during the peak-nesting season. No documented nesting females were preved upon, but 2 of 3 female mortalities attributed to mammalian predators were found in upland areas suitable for nesting. High mortality of adult females relative to males during the breeding season is a major cause of skewed sex ratios among Holarctic dabbling ducks (Johnson and Sargeant 1977; Blohm et al. 1987; Brasher et al. 2006; Arnold et al. 2012) and birds in general (Donald 2007). It is possible the high rate of botulism mortality during our study attenuated an overall sex effect on survival; and in years without severe botulism outbreaks, sex-specific variation in survival may occur. Additionally, low apparent nesting propensity among our sample of birds  $(\leq 20\%)$  limited our ability to test for an effect of life history stage (e.g., incubation) on survival. Thus, we cannot rule out sex-specific variation in adult mortality - and more



**FIGURE 3.** Predicted values of the monthly number of botulismrelated dead and sick Hawaiian Ducks (with 95% confidence intervals) in relation to concurrent-lagged rainfall at Hanalei National Wildlife Refuge, Kaua'i, Hawai'i, USA, 2013–2014. Estimates are derived from the top-ranked model (log<sub>e</sub>(count) =  $\beta_0 + \beta_1 * sur$  $veillance time + <math>\beta_2 * rainfall_{concurrent-lagged} + \beta_3 * rainfall_{concurrent-lagged}^2$ ), including minimum (59 hr), mean (118 hr), and maximum (271 hr) values of monthly surveillance time in panels (**A**), (**B**), and (**C**), respectively. Black points indicate actual values.

specifically, predation risk – as one possible mechanism for the apparent skewed sex ratio (>2:1) observed on northern Kaua'i.

Predation accounted for 31% (n = 5) of mortalities with known causes for adult Hawaiian Ducks, and we attributed most events to non-native mammals. The mammalian predator community posing risk to adult ducks on Kaua'i is likely limited to cats, dogs, and feral pigs, and characteristics of birds that were presumably preved upon by mammals in this study were most consistent with cat kills (e.g., clusters of sheared feather vanes, wings gnawed off at shoulder joint, carcass thoroughly fed upon, all or majority of flesh chewed off bones, bones broken and gnawed; Einarsen 1956; Bumann 2002). Previous work suggests that cats prey upon Hawaiian Duck eggs and chicks (Engilis Jr. et al. 2020; Malachowski et al. 2018; USFWS 2011), and our results indicate risk to adult birds should also be a serious consideration for managers. Non-native mammalian predators can be particularly impactful to island-endemic bird species and have been directly linked to several extirpations and extinctions (Nogales et al. 2004). Refuge management includes feral cat control, and active trapping occurred during our study period. But Hawaiian Ducks move beyond the refuge boundaries, and all putative cat predations on radio-tagged birds occurred on private lands suggesting efforts to co-manage feral cats on federal and private lands are needed if the goal is to minimize this mortality source to the population of Hawaiian Ducks using Hanalei NWR. Avian predators were implicated in 1 of the 5 predation events and likely attributable to 1 of the 2 resident raptor species that occur on Kaua'i: the introduced Barn Owl and the endemic Hawaiian Short-eared Owl. Dietary analysis using noninvasive genetic sampling methods may help clarify the relationship between owls and Hawaiian waterbirds where species co-occur.

The disparity in adult survival between Hawaiian Ducks and North American Anas is likely due to lower predator diversity and density, absence of hunting, and more stable resource conditions on Kaua'i compared to continental North America (Schwartz and Schwartz 1953, Swedberg 1967; Devries et al. 2003; Bielefeld and Cox 2006; Fleskes et al. 2007; Dooley et al. 2010; USFWS 2011; Arnold et al. 2012; Malachowski et al. 2019), whereas the difference with Laysan Ducks is likely because Laysan Ducks occupy remote atolls where mammalian predators are absent and avian predators are infrequent (Reynolds 2002; Reynolds and Citta 2007; Reynolds et al. 2008, 2015). However, demographic rates of Laysan Ducks vary between islands, and populations in botulism-prone ecosystems (e.g., Midway Atoll) can have lower adult survival than on Laysan Island (Reynolds et al. 2020). Several studies suggest island endemic ducks generally possess K-selected traits of high adult survival and low reproductive output (Cody 1966; Lack 1970; Moulton

and Weller 1984; Reynolds and Citta 2007), and population growth rates for species exhibiting these traits may be particularly sensitive to changes in adult mortality (Stahl and Oli 2006). Estimates for additional demographic parameters (e.g., nest success, brood and juvenile survival), along with sensitivity analyses, would be useful for assessing the relative importance of our adult survival estimates for Hawaiian Duck population dynamics.

Our results indicate that current refuge management actions to control feral cats and manage botulism risk are targeted at the primary causes of adult mortality. Carcass density is associated with risk of mortality in avian botulism outbreaks (Evelsizer et al. 2010b), and management actions currently include year-round surveillance for outbreak detection and searches to recover sick birds and carcasses to reduce the carcass-maggot cycle and toxin spread through the food web (Reed and Rocke 1992; Wobeser 1997a; Evelsizer et al. 2010b; USFWS 2011). Although carcass detection and removal using traditional search methods is not feasible in some wetland systems because of their large size (Evelsizer et al. 2010a) and dense vegetation (Cliplef and Wobeser 1993; Rocke and Bollinger 2007), removal is a viable tool for managing botulism in small wetlands under intensive monitoring, such as those at Hanalei NWR (Rocke and Bollinger 2007; Work et al. 2010; Reynolds et al. 2021). Nevertheless, effort associated with traditional surveillance methods can be a prohibitive factor (e.g., 2,823 person-hr during our 2-year study), highlighting the need for more efficient surveillance methods (Reynolds et al. 2021). Additionally, we recommend improvements of the water infrastructure and nutrient management associated with taro lo'i that can increase the capacity to flush and drain fields to help reduce botulism outbreaks while protecting receiving waters. Such actions would benefit the lower watershed and the entire suite of endangered Hawaiian waterbirds and the Hawaiian Goose. Our results provide insight on year-round management of botulism risk for nonmigratory waterbirds in tropical regions.

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