

Application of the complete-data likelihood to estimate juvenile and adult survival for the endangered Hawaiian stilt

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Abstract

Applied ecologists routinely use demographic models to predict population trajectories. Survival rates throughout the life cycle, which are required for these models, are often difficult to obtain, especially for long-lived or mobile species. Detailed information for pre-adult age classes in particular is often lacking. Using a 20-year dataset from several hundred individuals, we used Markov chain Monte Carlo methods to fit hierarchical models that describe survival rates for both adult and sub-adult Hawaiian stilts *Himantopus mexicanus knudseni*, an endangered island endemic. We constructed the complete-data likelihood and used data augmentation to estimate missing values and incorporate data that were not collected during formal sampling. Survival estimates were lower and more uncertain during the first 2 months of life compared with the remainder of the first year. The probability of first-year survival averaged 0.55 (95% credibility interval: 0.07–0.90), but varied considerably among cohorts from different years and islands. Probability of adult annual survival differed little between females (0.79; 0.71–0.86) and males (0.80; 0.72–0.87), but increased as birds aged from 1 to 20 years (0.77–0.85). Our analysis confirms that earlier work, despite being based on few data, provided good point estimates for survival rates. Our new analysis, however, provides the first comprehensive assessment of uncertainty in survival rates and detailed information on the nature of variation in first-year and adult survival. This information will help inform new demographic models and can be used to guide management actions.

Introduction

Demographic modeling is critical to applied population management (Getz & Haight, 1989; Reed *et al.*, 2002; Beissinger *et al.*, 2006). Survival rates can be difficult to determine, especially for species in which individuals disperse beyond the limits of the study area (e.g. Koenig, van Vuren & Hooge, 1996). Consequently, population growth and viability models are often made with survival data of questionable quality. Survival information also is frequently limited to adult life stages, and although this period can have the greatest influence on population persistence, understanding juvenile survival can provide important insights into management actions that affect population

growth (Crouse, Crowder & Caswell, 1987; Fefferman & Reed, 2006).

For long-lived vertebrates, information on patterns of juvenile survival within the first year is especially lacking. In birds, for example, it is widely documented that juvenile survival rates are lower than corresponding adult values (Lack, 1954; Newton, 1979; Johnson, Nichols & Schwartz, 1992), but few studies have documented fine-scale details of survival after fledging. Consequently, in population models, first-year survival rate is often assumed to be some fixed fraction of adult survival (e.g. Lloyd *et al.*, 2005). With growing interest in understanding what happens during the immediate post-fledging period (Reed *et al.*, 1999a; Fletcher, Koford & Seaman, 2006; Berkeley, McCarty &

Wolfenbarger, 2007), and constantly improving means of tracking individuals (e.g. Wiens, Noon & Reynolds, 2006; Yackel Adams, Skagen & Savidge, 2006; Suedkamp Wells *et al.*, 2007), knowledge of this life stage is improving. Most studies, however, still do not and often cannot track individuals for more than a few weeks after leaving the nest (e.g. Anders *et al.*, 1997; but see, e.g., Borkhataria *et al.*, 2012; Dwyer, Fraser & Morrison, 2012).

In the mid-1990s, we conducted a population viability analysis for the endangered Hawaiian stilt *Himantopus mexicanus knudseni* (Reed, Elphick & Oring, 1998). This subspecies of the black-necked stilt is endemic to the main Hawaiian Islands and is listed as endangered under the US Endangered Species Act. At that time, detailed information on survival was lacking, and inferences were made from only 2 years of banding data and information from other large shorebirds. Subsequently, many birds were marked and a large mark-recapture dataset created. During this time, considerable effort also has been put into improving statistical models of survival to account for imperfect detection and to better use the available information (e.g. Sandercock, 2006). Recently, Markov chain Monte Carlo methods have made it possible to fit complex hierarchical models to mark-resighting data (Schofield, Barker & MacKenzie, 2009). This approach is beneficial (Link *et al.*, 2002; Royle, 2008; Gimenez *et al.*, 2009) because it allows one to construct the complete-data likelihood (*sensu* Little & Rubin, 1983), which is otherwise intractable for complex problems, and to separate the detection and survival processes (Gimenez *et al.*, 2007; Schofield *et al.*, 2009). The complete-data likelihood includes missing values using data augmentation, and is therefore more complete than alternative analytical methods. This approach can improve parameter estimation by including latent variables (e.g. sex when not known for some individuals, which otherwise results in biased estimates when individuals of unknown sex are omitted from an analysis; Nichols *et al.*, 2004) and auxiliary encounter data that were not collected as part of the primary sampling scheme (e.g. individuals detected after formal sampling ends).

Here, our primary objective is to use a 20-year mark-resighting dataset that samples from the entire population of the endangered Hawaiian stilt *Hi. mexicanus knudseni* to estimate both monthly survival over the first year of life and annual survival thereafter. To achieve this aim, we apply hierarchical models that use the complete-data likelihood, allowing incorporation of auxiliary encounter data and independent variables that contain unknown values. These analyses allow us to evaluate previous results that were based on limited survival data (Reed *et al.*, 1998).

Methods

Study system

Hawaiian stilts are an endangered subspecies of bird endemic to the main Hawaiian Islands. There are few population size estimates before the 1940s, although Henshaw

(1902) reported stilts as common on Oahu in the late 1800s, but scarce by 1900. Munro (1944) estimated that numbers range-wide had dropped to ~200 individuals by the 1940s. Following cessation of hunting in 1939, numbers rose rapidly, and by 1947 there were around 1000 individuals (Schwartz & Schwartz, 1949). Subsequently, the population has increased to ~1500 birds, but the subspecies remains listed as endangered (Reed *et al.*, 2011; U.S. Fish and Wildlife Service, 2011).

Data collection

Survival during the first year was estimated from birds banded as chicks and surveyed regularly over the following 18 months; subsequent observations of these birds were treated as auxiliary data in our analyses. Hawaiian stilts nest primarily from March to early October, with a peak in mid-May to July (Robinson *et al.*, 1999). Most birds were banded in May–July, at ages 1–3 weeks post-hatch, based on known hatch dates or morphological traits (Reed *et al.*, 1999b). Chicks leave the nest immediately after hatching and feed in open habitat. Birds were captured by hand following observations in known nesting areas and received three colored Darvic bands and one aluminum numbered leg band. Monthly survival was estimated from 266 chicks in eight cohorts from the islands of Hawaii, Oahu and Molokai (see Supporting Information Appendix S1). In 1994 and 1995, 191 chicks were banded on Oahu, in and around the James Campbell and Pearl Harbor National Wildlife Refuges and at Rowland's Pond (an oil settling pond owned by Chevron Products Company). In 1998 and 1999, 45 chicks were banded at artificial ponds created by Cyanotech Corporation on Hawaii. Finally, during 2008–2011, 30 chicks were banded at Ohiapilo Pond Bird Sanctuary, the Kaunakakai Wastewater Reclamation Facility and other small wetlands on Molokai.

For the Oahu and Molokai cohorts, at least weekly surveys to relocate banded birds were conducted at wetlands island wide. During these surveys all major wetlands used regularly by stilts were surveyed. In addition, wetlands on Oahu where most banding was performed received additional surveys, and opportunistic observations were made throughout the state. If a banded bird was seen at any time during the month, it was recorded as having survived to that month. For the 1994 and 1995 cohorts, additional statewide surveys were conducted monthly for a year after banding. For the Hawaii cohorts, during 1998–2000 at least monthly surveys were conducted at the banding site, at Kealahou Wastewater Treatment Plant, and when possible at the nearby Aimakapa and Opaepa Ponds.

Annual adult stilt survival was estimated on all main islands using observations of the same cohorts plus additional birds banded as 1- to 3-week-old chicks on all main islands after 1992 (see Supporting Information Appendix S1). From July 1994 until June 1996, monthly surveys were conducted statewide, although not all wetlands were accessible on every trip, and some wetlands were inaccessible. Surveys were not carried out on Lanai or Niihau; the

former because few birds occurred on the island and the latter because the island is privately owned. Niihau stilts, however, migrate seasonally to Kauai (Engilis & Pratt, 1993), where wetlands were surveyed. In addition to the 1994–1996 surveys, we incorporated resightings from many other observations made during 1993–2012. Banded birds were also reported during statewide Biannual Waterbird Surveys coordinated by the Hawaii Division of Forestry and Wildlife. Permanent emigration from the main Hawaiian Islands is unknown and our sampling encompassed all major and most minor sites where members of the marked population might occur. Stilts banded in the 1970s (Coleman, 1981) and seen during our study contributed information on longevity, but not to survival estimates because resighting was minimal and sporadic before the 1990s. If a banded bird was seen at any time during the calendar year after banding, it was recorded as having survived. After the Basic I molt, Hawaiian stilts can be sexed by plumage (Reed *et al.*, 1999b), allowing separate estimates of survival for males and females.

Statistical analyses

To estimate survival we used open population models using the complete-data likelihood (Gimenez *et al.*, 2007; Schofield *et al.*, 2009). We estimated monthly juvenile survival, examining differences among months and cohorts using the following model:

$$\gamma_{1c_i} \sim \text{norm}(0, \tau)$$

$$\gamma_{2m} \sim \text{norm}(0, \omega)$$

$$\beta_{1t} \sim \text{norm}(0, \xi)$$

$$\text{logit}(S_{i,m})_{\text{chick}} = \gamma_0 + \gamma_{1c_i} + \gamma_{2m}$$

$$a_{i,m} \sim \text{Bern}(S_{i,m} a_{i,m-1})$$

$$\text{logit}(p_{i,m})_{\text{chick}} = \beta_0 + \beta_{1t} + \beta_{2\text{Oahu}_i} + \beta_{3\text{Molokai}_i}$$

$$\text{data}_{\text{chick}} \sim \text{Bern}(p_{i,m} a_{i,m}).$$

Survival (S) of individual i was a function of cohort c and age in months (m), both modeled as random effects. Detection (p) was a function of island, in order to account for differences in search strategy and wetland area on each island, and study month (t), with separate random effects for each month during the study. τ , ω and ξ are variance parameters for the random effects. Auxiliary sightings of chicks seen after the period of intensive resighting were incorporated via matrix \mathbf{a} (after Schofield *et al.*, 2009). Survival from banding through the end of the first year was calculated as the product of monthly survival rates. There are good reasons to expect survival to vary among islands and years (e.g. variation in predation risk), but cohorts on

different islands came from different years, so there was no way to distinguish these sources of variation. In contrast, we had no *a priori* reason to expect detection rates to differ among years on an island because survey methods were similar within islands and our experience suggested no major environmental changes that would affect detection. Consequently, we did not include separate intercepts for each cohort on an island.

We estimated annual adult survival, including effects of sex, calendar year (t), and age (in years) in the model. Detection was modeled as a function of rainfall and calendar year:

$$\gamma_{2t} \sim \text{norm}(0, \tau)$$

$$\beta_{2t} \sim \text{norm}(0, \omega)$$

$$\text{sex}_i \sim \text{Bern}(\psi)$$

$$\text{logit}(S_{i,t})_{\text{adult}} = \gamma_0 + \gamma_1 \text{sex}_i + \gamma_{2t} + \gamma_3 \text{age}_i$$

$$a_{i,t} \sim \text{Bern}(S_{i,t} a_{i,t-1})$$

$$\text{logit}(p_{i,t})_{\text{adult}} = \beta_0 + \beta_1 \text{rainfall}_t + \beta_{2t}$$

$$\text{data}_{\text{adult}} \sim \text{Bern}(p_{i,t} a_{i,t}).$$

τ and ω are variance parameters for the random effects. Because sex was unknown for some individuals, we used data augmentation using matrix \mathbf{a} to assign missing values using a uniform prior from 0 to 1 for sex ratio (ψ). We assessed whether adult detection differed among years, because much of the resighting effort was *ad hoc* and thus potentially variable. Also, we tested whether annual rainfall affected detection because it has been suggested as a concern for population surveys (Engilis & Pratt, 1993; but see Reed *et al.*, 2011). Rainfall data were obtained from National Oceanic and Atmospheric Administration and were statewide annual totals (see Supporting Information Appendix S1).

Model selection and validation are not straightforward for complex hierarchical models (Gelfand & Ghosh, 1998; Schofield *et al.*, 2009). A commonly used method is the deviance information criterion, a generalization of Akaike's information criterion (Spiegelhalter *et al.*, 2002), but this approach is problematic for complex hierarchical models (Plummer, 2008). An alternative, Bayes factors, is also controversial and difficult to calculate for complex models (Link & Barker, 2006; Schofield *et al.*, 2009). As an alternative to choosing among candidate models, to test the importance of the sex and age effects, we fitted the full model as well as a suite of reduced models to determine whether estimates of adult survival were sensitive to which variables were included (Gelman *et al.*, 2004). This approach was tractable because our models contained relatively few independent variables, and therefore a small number of possible combinations: the full model (specified in the equations above), and reduced models describing either a single

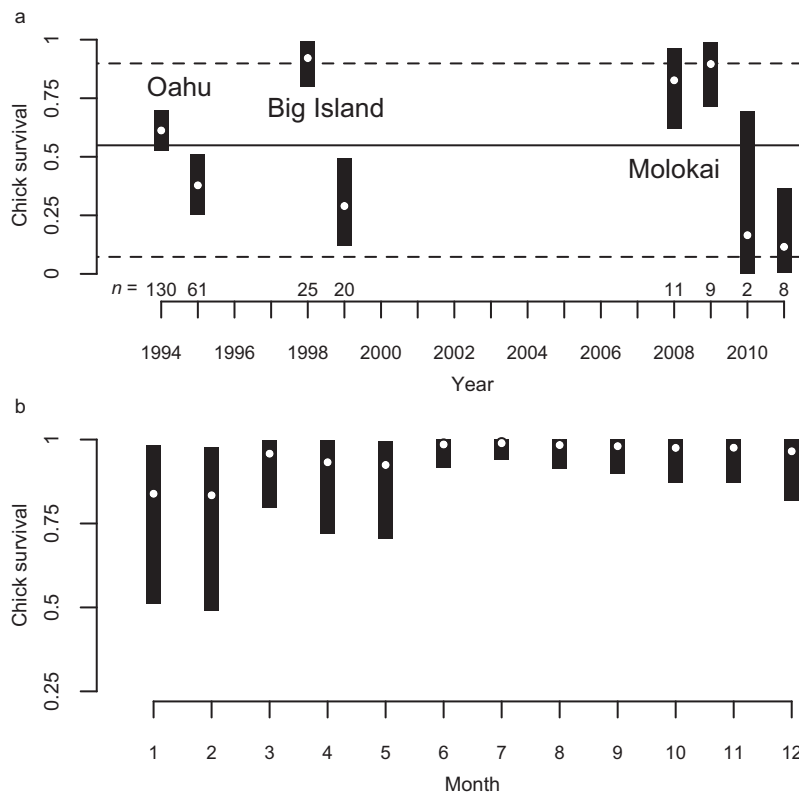


Figure 1 Results from first-year survival model for eight cohorts of Hawaiian stilts banded during their first month of life. Cohorts come from three of the islands where stilts breed (Oahu, Hawaii, Molokai), each sampled during different years. Survival was allowed to vary among cohorts and months: (a) estimates for each cohort; (b) estimates for first 12 months of life after banding. White dots indicate means with black bars showing 95% credible intervals; solid horizontal line in (a) indicates cumulative annual survival rate with dotted lines indicating the 95% credible interval; sample sizes for each cohort are given below each bar in (a).

estimate of adult survival, survival varying with age or survival separated by sex, with each of these four models repeated with and without detection dependent on rainfall. Models were fit using JAGS (version 3.2.0; Plummer, 2003) in R with the R2jags package. We ran three chains for each model with a burn-in period of 50 000 iterations. Chains were run for 100 000 iterations or until the potential scale reduction factors for all parameters were <1.01 (Brooks & Gelman, 1998). Uninformative priors were used for all intercepts, variance parameters and sex ratio (adult model). All continuous fixed effects were standardized on a scale from 0 to 1. Uncertainties in parameter estimates taken from posterior distributions are expressed as 95% credible intervals (CI; See Supporting Information Appendix S1).

To evaluate the models, we compared the resighting matrix to model predictions and checked for systematic bias and overdispersion (Gelman *et al.*, 2004; Gelman & Shalizi, 2011). An advantage of estimation via MCMC is that it is straightforward to calculate the posterior distributions of relevant test statistics from within the model code. These distributions can then be compared with the observed data. For survival models, the sums of the columns and rows of the mark-resight matrix provide logical test statistics that are simple to obtain. Summing by columns or rows, respectively, provides replication by individuals and either years (for the adult model) or months (for the juvenile model). Observed data points that fall outside a prediction interval provide evidence of overdispersion with respect to the model's sampling variance.

Results

The 266 chicks that were individually color banded and followed via intensive resighting efforts produced 819 resighting months of birds less than a year old, where multiple sightings of a bird in the same month counted as one resighting month. We estimated first-year survival to be 0.55 (95% CI: 0.07–0.90; Fig. 1a), with lower estimated monthly survival and higher uncertainty during the first 2 months compared with subsequent months (Fig. 1b). Survival during the first year varied considerably among cohorts, ranging from very high (0.92, 0.80–0.99) on Molokai in 2009 to almost complete failure on the same island the following 2 years (Fig. 1a). Small sample size may account in part for cohort variation (e.g. 2010), but the lack of overlap in CIs suggests that this alone cannot account for differences.

The larger dataset of 543 birds, all banded as chicks, produced 779 resighting years during 1994–2012 that were used to estimate annual adult survival. The oldest females in our study were last seen 16 and 19 years after hatch. At least six males lived at least 16 years, of which two were recorded 16 and 20 years after being banded as chicks. **The others were banded as adults prior to our study and were observed alive 19, 20, 23 and 29 years after banding.**

Adult survival was similar for both sexes, with estimates of 0.79 (0.71–0.86) for females and 0.80 (0.72–0.87) for males (Fig. 2a,b). Consistent with this result, the posterior distribution for the adult sex ratio suggests little deviation from 1:1 (Fig. 2c). Survival rate differed with age, increasing

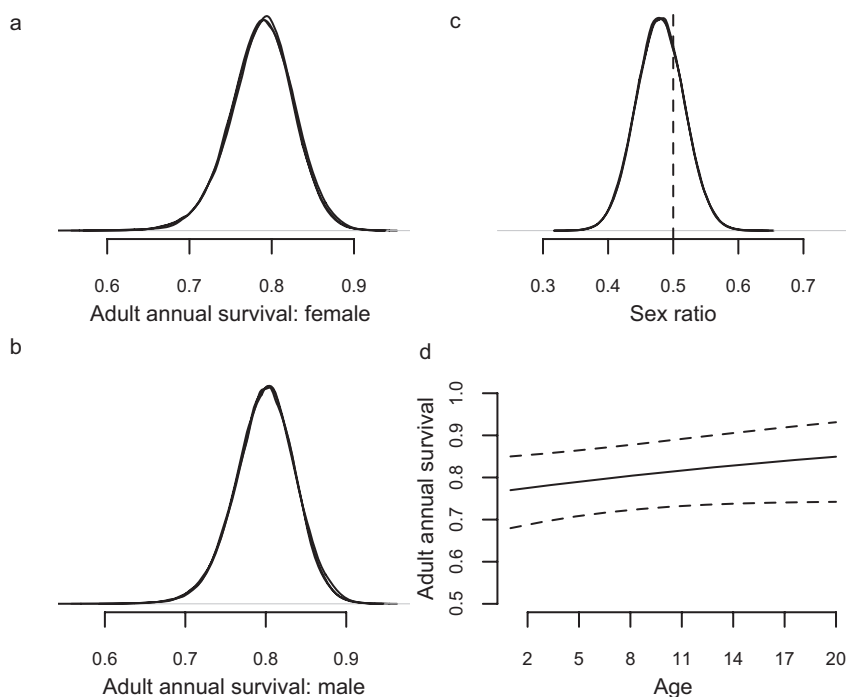


Figure 2 Results from adult survival model for Hawaiian stilts, in which survival is allowed to vary between males and females, among calendar years, and with the birds' age: (a) female survival; (b) male survival; (c) estimated sex ratio; (d) age-related variation in adult survival. The heights of the curves in (a–c) represent the likelihoods of a given value for each survival estimate; results of three replicate likelihood estimates (chains) are shown in each plot to illustrate the high degree of overlap. Dashed lines in (d) show the 95% credible intervals.

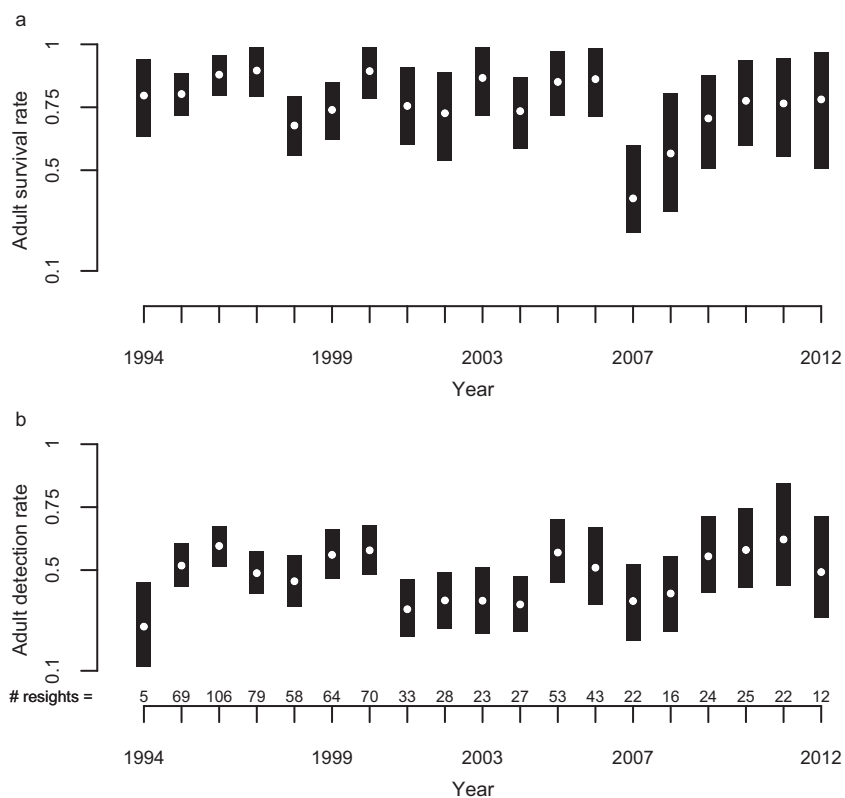


Figure 3 Estimates of (a) survival and (b) detection rates, by calendar year, for adult Hawaiian stilts banded during their first month of life. White dots indicate means with black bars showing 95% credible intervals; numbers of birds resighted in each year are given above the x-axis in panel (b).

from 0.77 (0.68–0.85) between the first 2 years to 0.85 (0.74–0.93) between ages 19 and 20 (Fig. 2d). Adult survival also fluctuated among calendar years but with no clear trend (Fig. 3a). Annual detection for adult stilts varied among

years (Fig. 3b), but the analysis provides only weak support for the hypothesis that annual rainfall negatively affects detection ($\text{Pr}(\text{regression coefficient for rainfall} < 0 \mid \text{data}) = 0.77$).

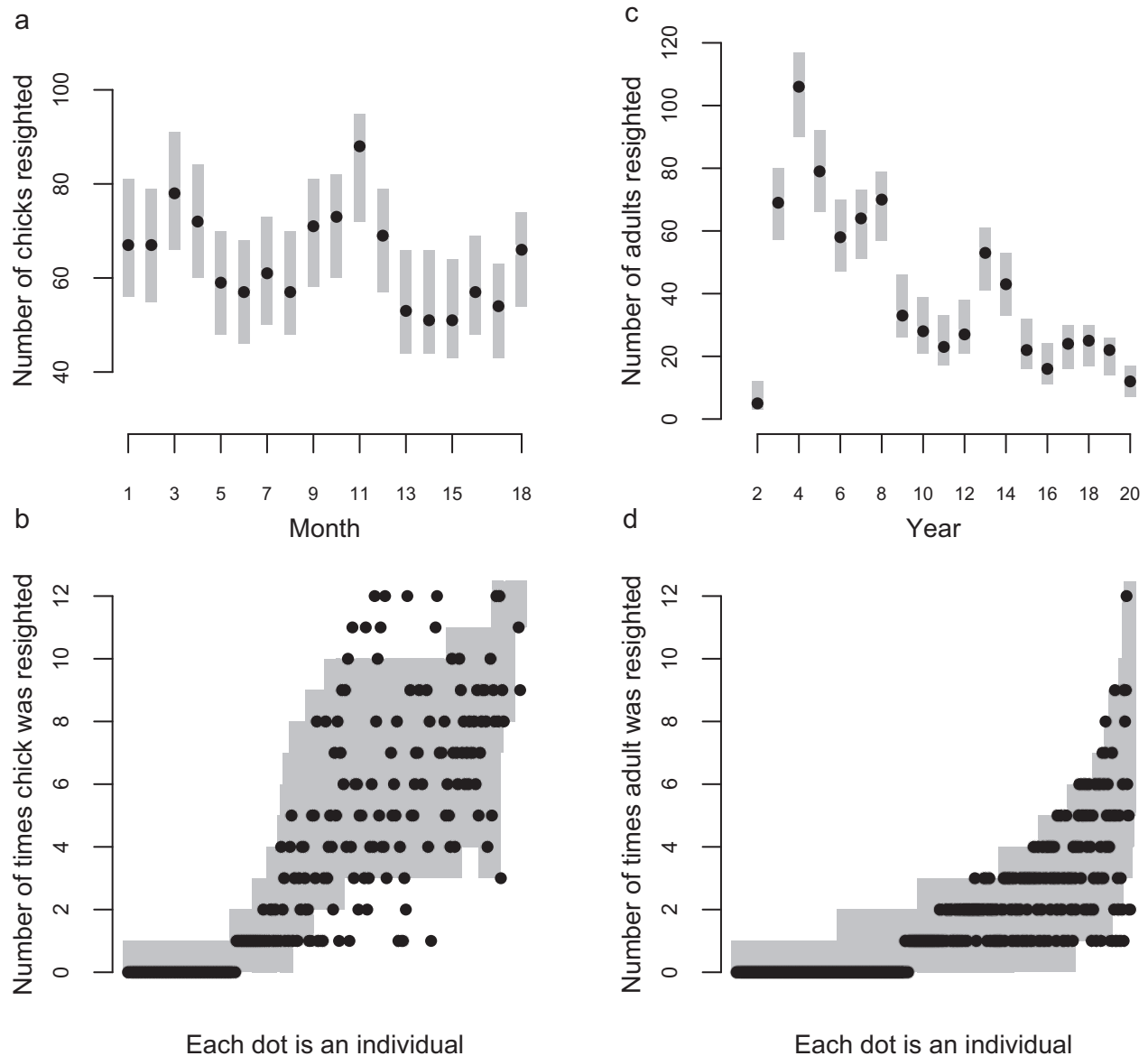


Figure 4 Posterior-predictive checks to evaluate the fit of the best survival models for first year (a, b) and adult (c, d) Hawaiian stilts. The 95% prediction intervals are shown as gray bars, with the observed values of the test statistics plotted as black dots. The uncertainty in the predictions comes from the sampling variance of the Poisson binomial distribution, rather than model error. The top two panels compare, for each model, the number of individuals resighted in each time period to the number predicted. The bottom two panels compare the number of times each individual was resighted to the corresponding prediction.

Posterior-predictive checks show that the number of birds resighted in a given month or year fell well within the predicted ranges (Fig. 4a,c). For the adult survival model, the number of times each individual was resighted fell within the predicted range 97% of the time, suggesting no overdispersion (Fig. 4d). The first-year survival model, in contrast, showed some overdispersion with 14% of observed resighting rates falling outside the predicted range. This means that there was some individual variation in the chick model that was not accounted for; however, the evidence suggests no systematic bias (Fig. 4b).

Comparison of alternative model structures suggested that estimated survival is insensitive to model structure (Fig. 5). Only the credibility intervals associated with age are noticeably different, and then only when the very oldest and youngest ages are compared and with much overlap remaining (see also Fig. 2d).

Discussion

Despite extensive statistical methods development, uncertainty over which survival models are best and the

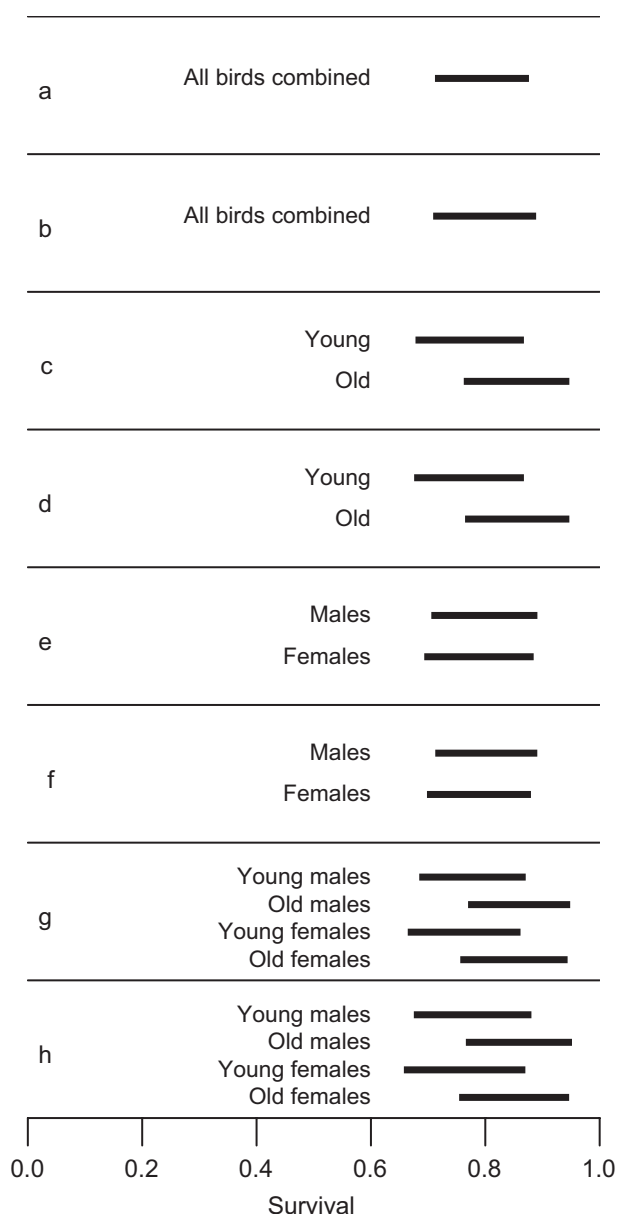


Figure 5 Adult survival estimates produced with alternative model structures (black bars represent 95% credible intervals): (a) single estimate for all individuals, with detection constant; (b) single estimate for all individuals, with detection dependent on rainfall; (c) survival varies with age, detection constant; (d) survival varies with age, detection dependent on rainfall; (e) survival varies between sexes, detection constant; (f) survival varies between sexes, detection dependent on rainfall; (g) survival varies with age and between sexes, detection constant; (h–j) full model, in which survival varies with age and between sexes, detection dependent on rainfall. ‘Young’ and ‘old’ represent estimates for the youngest (age 1–2) and oldest [age (19–20) individuals, i.e. the end points of the continuum shown in Fig. 2d].

ever-increasing mathematical complexity of methods can limit their use (cf. LaDeau, 2010). It is important, then, to ask how much increased model sophistication affects the biological inferences made. We found that the point estimates for Hawaiian stilt survival produced in the current analysis, based on a 20-year dataset, were almost identical to those from uncorrected resighting rates based on only 2 years of data (Reed *et al.*, 1998). This result might be unsurprising for adults given the narrow distribution of likely values (Fig. 2). In contrast, the close estimate of first-year survival was serendipitous given the high variance among cohorts (Fig. 1a). Despite the similarities, evaluating the previous survival estimates using more sophisticated methods and a better dataset gives credence to the earlier estimates and the resulting population viability analysis, which is especially important because sensitivity analyses suggested that viability predictions were more sensitive to error in adult survival than to errors in other parameter estimates. Viability assessments are also affected by parameter variance, with greater variance associated with lower viability (Beissinger & Westphal, 1998; Reed *et al.*, 2003). The current analysis provides a substantially better understanding of variation in survival rates, which will allow for improved viability assessments in the future. The new analysis also identified a small, but steady, increase in annual adult survival with age (Fig. 2d), which contrasts with the commonly reported constant (e.g. Weimerskirch, 1992), or decreasing (e.g. Holmes, Flückiger & Austad, 2001) survival rates of adult birds. As we only fit a model with a linear trend for age (because a more complex model based on a spline would not converge), we cannot rule out that survival does not decrease at the oldest ages. It is unlikely that our result was caused by increases in site fidelity with age because our sampling included most breeding areas within the subspecies’ range.

We found little support for the notion that rainfall affects detectability of Hawaiian stilts. We included this parameter in our analyses because prior population trend assessments suggested a link between higher rainfall and decreased survey numbers, perhaps because stilts spread out across the landscape more in wet years, thus reducing detectability (Engilis & Pratt, 1993; Reed *et al.*, 2007). Our result, however, is consistent with a more recent analysis of population trends (Reed *et al.*, 2011), which used a longer time series and more resolved rainfall data, and revealed no association between abundance and rainfall.

Juvenile survival is important in population models, but data are often lacking and generally provide little temporal resolution. Recent avian studies using radio telemetry provide estimates of survival during the first few weeks after fledging (e.g. Naef-Daenzer, Widmer & Nuber, 2001), but few directly estimate monthly survival rates before adulthood. We found that survival rate and uncertainty improved after the first 2 months and was relatively constant thereafter (Fig. 1b). Similar patterns have been reported for red-billed choughs *Pyrhcorax pyrrhcorax* (Kerbiou & Julliard, 2010) and golden eagles *Aquila chrysaetos* (McIntyre, Collopy & Lindberg, 2006), where

survival rates are lower and more variable during the first 6 months after hatch, and in great bustards *Otis tarda* (Martin *et al.*, 2007) and wood storks *Mycteria americana* (Borkhataria *et al.*, 2012), which show steadily increasing survival rates. In contrast, young crested caracaras *Carcara cheriway* showed no differences in survival rate across months (Dwyer *et al.*, 2012). We also found high variation in survival rate among cohorts, which is likely due to idiosyncratic changes in the predator community and to the magnitude of predator control (e.g. Coleman, 1981). This variation was probably exacerbated by the small size of some of the cohorts analyzed.

One important caveat for our survival estimates is that most Hawaiian stilts occur in protected sites where management includes predator control and where public access is restricted. Non-native invasive species, such as mongoose *Herpestes javanicus*, cattle egret *Bubulcus ibis* and feral cat *Felis catus*, are important predators of stilts (Reed *et al.*, 2012). Even with extensive predator control, predation occurs, particularly of hatch-year birds (Coleman, 1981; Gassmann-Duvall, 1994; U.S. Fish and Wildlife Service, 2011). In the absence of active management, we expect survival rates to be considerably lower than the values reported here. Our results do not fundamentally change thinking on what managers are doing, but they do suggest that population viability models should be re-run to incorporate the current information on variation and uncertainty in survival. A longer time series provides more accurate, and typically larger, estimates of variation for demographic parameters, leading to more accurate and typically more conservative estimates of viability (Reed *et al.*, 2003).

Advancing survival analysis clearly depends on improved data collection and appropriate model use. In our case, improvements were primarily in the ability to quantify parameter uncertainty. Bayesian estimation methods allow full quantification of uncertainty for parameters of interest, and they allow techniques such as data augmentation to construct the complete-data likelihood, which makes better use of all available data (e.g. Shoemaker *et al.*, 2013). When using popular Markov chain Monte Carlo samplers (such as JAGS and BUGS <http://www.mrc-bsu.cam.ac.uk/bugs/>), generating model predictions from the posterior predictive distribution is often readily accomplished with a few lines of code. These predictions can be checked against the observed data to help point to the most important areas for model refinement (Gelfand & Ghosh, 1998; Gelman *et al.*, 2004). Using posterior predictive checks to identify when models produce poor predictions is especially important for population models, because it might affect management decisions. For example, the checks on our model for first-year survival show evidence of overdispersion (Fig. 3b), which suggests that if using these data for population projection models one should build in individual variation in chick survival. In contrast, posterior checks of our adult survival model suggest little additional value to increasing model complexity. Similarly, our comparison of credibility intervals produced by alternative model structures reinforces the notion that our parameter estimates are not especially sen-

sitive to the exact model formulation. The ability to use all available data can also improve parameter estimates. For example, for our first-year survival estimates, we were able to draw on the 'borrowing strength' from additional sightings made after the first year (cf. Cam, 2012). Further advances in survival analysis are likely to rely on similar innovations that allow us to get more information from the data we collect.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Application of the complete-data likelihood to estimate monthly juvenile and annual adult survival for endangered species management.

Table S1. R code for analysis.

Table S2. Adult meta-data.

Table S3. Adult resighting data used in the analyses.

Table S4. Chick meta-data.

Table S5. Chick resighting data used in the analyses.

Table S6. Rainfall data used in the analyses.