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Estimating the survival of unmarked young from repeated counts

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Estimating the survival of juveniles is important to the study of ecology and wildlife management. Methods to estimate survival from uniquely marked young are generally preferred but may be difficult to implement. Alternative methods to estimate juvenile survival based on counts of unmarked young with marked parents generally do not account for detection probability or encounter difficulty estimating survival when there are >5 offspring. We developed a hierarchical Bayesian model to estimate survival of unmarked offspring from known (marked) parents from a minimum of two counts on while accounting for imperfect detection. We simulated data to evaluate the performance of the model across a range of detection probabilities and sample sizes and to explore violations of some model assumptions. We then demonstrate the utility of this approach by estimating chick survival for a population of ring-necked pheasants *Phasianus colchicus* in east-central Illinois, USA. Mean error of parameter estimates decreased with increasing sample sizes and detection probability and was greater for covariate coefficients, compared to mean detection or survival probabilities. However, posterior distributions of mean survival and detection parameters were poorly estimated and had small effective sample sizes when the mean detection probability was ≤0.4 or the number of broods comprising the sample were <30. The model was relatively robust to violations of the model's closure assumption, with a <0.04 increase in bias of detection and survival probabilities when survival between repeated counts was <1. When applied to our data set of 38 pheasant broods, we were able to identify important temporal and environmental covariates affecting survival and detection. Mean detection probability was only 0.56. We believe the coupling of this model with an appropriate field sampling framework provides a useful and flexible approach that is time- and cost-efficient for estimating survival of unmarked young.

Keywords: brood flush, chick survival, detection probability, flush count, juvenile survival, ring-necked pheasant

Survival of juvenile offspring is an important, often overlooked and poorly studied component of population dynamics. Population growth rates are often sensitive to survival of young and accurately estimating survival during this period is critical for the management of species of concern and game animals (Clark et al. 2008, Dreitz 2009, Davis et al. 2016). Multiple methods exist to estimate survival of individuals that are uniquely marked with bands or radio transmitters (Williams et al. 2002, Silvy 2012). Although uniquely marking and following individuals may be preferred, due to less uncertainty in individual fate and simplified analysis, there are drawbacks to this approach. For instance, markings can adversely affect survival or behavior (Mong and Sandercock 2007, Amundson and Arnold 2010, Barron et al. 2010), may be only practical for conspicuous species (Dreitz 2009, McCaffery et al. 2016), or may require a large investment of personnel, time and money, which may not be feasible in many studies. Consequently, less resource-intensive methods of estimating the survival of young are needed.

When young are not marked but their parents are, survival can be estimated from multiple counts of dependent young. Several methods using serial counts of young with marked adults have been developed, but these assume that detection is perfect (Flint et al. 1995, Manly and Schmutz 2001, Schmidt et al. 2010). For many species, and under many conditions, this assumption is difficult to fulfill (Pagano and Arnold 2009, Roche et al. 2014). We are aware of one model that estimates survival of unmarked dependent young while also accounting for imperfect detection (Lukacs et al. 2004). However, estimates from this model may be unreliable for animals that produce >5 offspring, especially when sample sizes are small (e.g. few flushes per brood, few broods; Lukacs et al. 2004). The uncertainty in estimation arises because the number of potential

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combinations of survival and detection that can produce the observed data increases when there are a large number of young, leading to convergence issues using maximum likelihood estimation (Lukacs et al. 2004). Consequently, this method may be impractical for studies of many species, such as game birds or waterfowl, without many broods and visits (Lukacs et al. 2004).

Among game birds, such as pheasants and other galliformes, the number of offspring per female typically exceeds five, parents and offspring are often cryptic, and frequent disturbance by repetitive flushes may not be desirable or practical. The lack of practical alternatives for estimating chick survival may contribute to the common practice of assuming perfect detection from counts of unmarked offspring groups (Pitman et al. 2006, Pollentier et al. 2014, Dyson et al. 2018), which can bias estimates of survival and related covariates, or collapsing offspring survival data into a binary state (Matthews et al. 2012, Wood et al. 2018), which obscures potentially important information about how many individuals may actually be alive. To provide a possible alternative, we developed a hierarchical model and sampling framework that uses Bayesian Markov-chain Monte Carlo (MCMC) methods to estimate the survival of chicks prior to independence, while accounting for imperfect detection.

The daily survival probability of young of pheasants and other precocial birds is often lowest early in life, but asymptotes to near 1, usually after one or two weeks post hatching (but prior to independence; Pietz et al. 2003, Lukacs et al. 2004, Davis et al. 2016). During the period of high daily survival, two or more counts of young made several days apart could be considered counts of a closed population. If the counts are performed at approximately the same age for all broods, they can be used to estimate chick survival during a period (e.g. first X days or Y weeks) of interest (Riley et al. 1998, Pollentier et al. 2014, Davis et al. 2016). Based on these assumptions, we simulated data across a range of plausible detection probabilities and violations of the closure assumption. We then applied the model to estimate the 15–22-day (three week) survival probability of ring-necked pheasant *Phasianus colchicus* chicks in east-central Illinois. Our purpose in developing the model was associated with research on pheasants, so we use terminology associated with gamebirds as a result.

Material and methods

Hierarchical models allow for complex problems or processes to be broken down into their smaller, more manageable parts. In ecology, hierarchical models are frequently employed to distinguish between the observed data, a product of imperfect detection of organisms, and a true, unobserved, state process such as animal abundance, survival probability or occupancy status (MacKenzie et al. 2002, Royle 2004).

Model

Our hierarchical model is a modification of a standard N-mixture model (Royle 2004), now comprised of two binomial models representing the apparent survival of a chick (state process) and the ability to detect an individual chick (observation process).

1. State process: $S_i \sim \text{Binomial}\left(H_i, \varphi_i\right)$
2. Observation process: $C_{ij} \sim \text{Binomial}\left(S_i, d_{ij}\right)$

The number of young surviving to the observation period for the *i*th brood, S_i, and apparent survival probability of a chick in the *i*th brood, φ_i, are latent variables, and H_i is the initial number of hatched offspring from the *i*th brood, typically inferred from the number of eggs that hatched. The number of observed chicks at visit *j* for the *i*th brood (C_{ij}) is a function of both the number of surviving chicks and the detection probability of a chick within the *i*th brood, on the jth visit, d_{ij}. Both apparent survival and detection probability can be modeled as a function of covariates using an appropriate link function.

Assumptions

The validity of the inference obtained from the model depends on several assumptions some of which are the same as those found in Lukacs et al. (2004):

1) All counts among broods (observations) are made at the same age or during a period when daily survival approximates 1, to minimize bias associated with varying exposure periods (e.g. 15–20 days).
2) There is no brood mixing between hatching and the final survey. Chicks that become separated from the brood before the first flush count are assumed dead.
3) Survival between the first and second counts is high enough to approximate a closed population.
4) Survival and detection probability are assumed homogeneous among broods, or accounted for via brood or survey-specific covariates.
5) Chicks within a brood are exchangeable (survival and detection are the same) and are not double counted during a flush.
6) The initial number of offspring is known.
7) The survival and detection of broods are independent of one another.
8) Young are still dependent on parents.
9) Parents can be located.

Simulated data and analysis

We demonstrate the performance of the brood survival model using 300 data sets simulated under 24 different scenarios. We held the number of observation periods, visits and mean number of chicks per brood constant (1, 2 and 13.75, respectively), while varying the number of broods monitored. Each scenario was a different combination of sample size (20, 25, 30, 35, 40 or 50 broods) and mean detection probability ranging from low to high ($\overline{d_{ij}}$; 0.2, 0.4, 0.6, 0.8). We restricted our simulations to a single observation period and two visits, though this framework can easily be expanded, similar to a robust design model (Pollock 1982), to allow for additional observation periods (primary periods) and visits within an observation period (secondary sampling periods; Fig. 1).

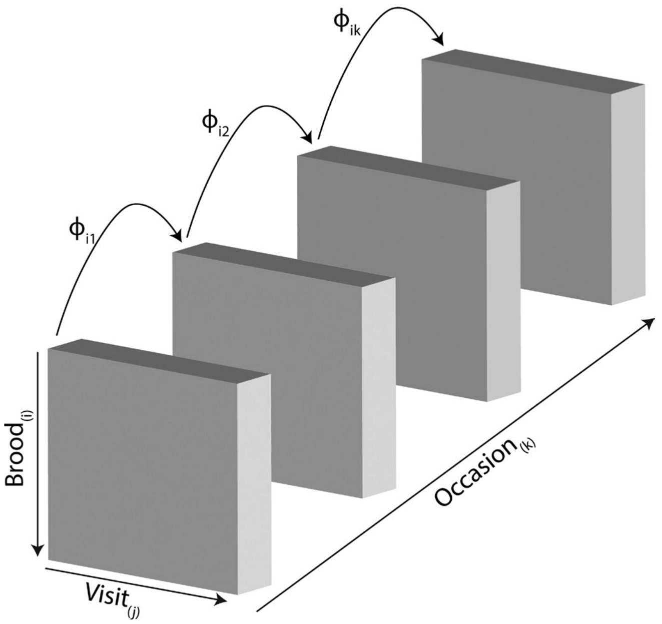

Figure 1. Diagram illustration how the data for the model can be organized and expanded beyond a single observation occasion (k) (primary period, sensu Pollock 1982) or more than two visits (j) (secondary periods, sensu Pollock 1982). In our example, there is only 1 primary period and 2 secondary sampling periods.

We simulated initial brood size (number of hatched chicks) by a random draw from the binomial distribution with size = 15 and probability = 0.85, adding one to ensure that all broods had at least one chick that hatched. We then simulated survival on the logit scale as the linear combination of a transformed mean survival probability ($\bar{\varphi} = 0.6$) plus a covariate representing a measure of habitat quality. The covariate was generated by a random draw from uniform (−2, 2) distribution, and the effect of habitat on survival was fixed at 0.8. We generated the number of chicks surviving to be observed through a random draw from the binomial distribution with size = initial brood size at hatch and probability = habitat-specific survival probability.

We used a similar approach to generate brood-visit specific detection probabilities. The detection covariate for each brood-visit was generated as a random draw from a uniform (−1, 1) distribution and the effect of this covariate was fixed at −1. This was combined in a logit linear model with the scenario-specific mean detection probability to get the true brood-visit detection probability. We then simulated the number of surviving chicks that were observed via a random draw from a binomial distribution with size = the number of chicks surviving to observation and probability = visit-specific detection probability (Supplementary material Appendix 1).

To test the robustness of our model to violation of the closure assumption, we performed an additional 300 simulations where survival between survey visits was not 1. We used a fixed sample size of 30 broods and $\bar{\varphi} = 0.6$. We simulated 12 different scenarios, varying daily survival (DSR; 0.99, 0.98, 0.97, 0.96) and the number of days between successive visits (one, three or four days between counts; Supplementary material Appendix 2). We performed all simulations in R ver. 3.5.0 (<www.r-project.org>).

Ring-necked pheasant data collection

We collected data on brood survival of ring-necked pheasants on 14 public and private grasslands in three different study areas in east-central Illinois. Grassland sites were located near the towns of Saybrook, IL (40°25′39″N, 88°31′36″W), Sibley, IL (40°35′15″N, 88°22′56″W and Chatsworth, IL (40°45′15″N, 88°17′35″W). Five sites were owned and managed by the Illinois Department of Natural Resources as Pheasant Habitat Areas. All remaining sites were privately owned and enrolled in the Conservation Reserve Program. Fields varied in size from ~16 to 260 ha. The landscape in which these sites are embedded is dominated by row-crop agriculture and >85% of the land cover is devoted to the production of corn *Zea mays* and soybeans *Glycine max* (Illinois Department of Agriculture 2000). Dominant vegetation cover among fields varied from native warm and cool season grasses and native forbs (e.g. *Sorghastrum nutans*, *Andropogon gerardii*, *Elymus canadensis*, *Solidago* spp., *Ambrosia* spp. and *Symphyotrichum pilosum*), to fields dominated by exotic grasses and forbs (e.g. *Bromus inermis*, *Setaria* spp., *Medicago sativa*).

We captured hen pheasants during four separate capture periods 26 September–21 October 2014, 13 January–30 March and 16 September–29 October 2015, and 27 January–28 March 2016. Pheasants were captured primarily via spot-lighting but also with walk in traps when snowfall was adequate (Labisky 1959). We attached a ~15 g or ~18 g, necklace-style radio transmitter (model series A3900 and A4000, Advanced Telemetry Systems, Inc., Isanti, Minnesota) to hens weighing >600 g to ensure that transmitter weight did not exceed 3% of the animal's body mass.

We tracked all hens from 1 April to 30 August 2015 and 2016, for 4–7 days per week until they began incubation and every 1–3 days thereafter. We located the nest bowl and examined the contents to determine the nest fate after hens left their nest. We classified nests as successful if ≥1 egg hatched and recorded the number of hatched eggs. We flushed each hen and brood one or two times, 15–22 days post hatch (~3 weeks) to count number of surviving young. We performed a second flush within four days of the first, but >90% flushes were completed within two days of the first. Because the majority of chick mortality occurs during the first two weeks post-hatching and chicks only become capable of sustained flight after ~12 days (Riley et al. 1998, Giudice and Ratti 2001). we were more likely to detect chicks and meet the necessary assumption of demographic closure between counts by estimating survival at ~3 weeks.

Broods were flushed by one or two observers and the number of chicks seen flying or running through the vegetation was recorded. We performed the majority of flushes from ~10 min before sunrise to ~20 min after sunrise, but several flushes occurred as late as ~3 h after sunrise. Because we believed that thick vegetation could reduce the detection probability, we measured vegetation density using a Robel pole (Robel et al. 1970) at the estimated roost location and at 4 m in each of the cardinal directions. We determined the roost location by marking the point where the hen flushed, began running or locating feces from the hen and chicks. We also created a binary variable, flush quality, where a 'good' flush corresponded to hens and broods flushing from an area ≤3 m in diameter ($n = 43$), and 'poor' flush corresponding to hens and chicks running through the vegetation or flushing at a distance of >3 m ($n = 25$).

We collected brood survival data from 23 broods in 2015 and 15 broods in 2016. In 2015, eight broods were flushed a single time while two broods were flushed only once in 2016. We omitted data where the hen was killed before we could flush the brood ($n = 3$) or where the eggshells were damaged, and we could not accurately count the number of hatched eggs ($n = 2$). We omitted broods where the hen was killed because we did not feel confident in assuming that all the chicks had died or that all chicks were able to survive. Thus, our estimate of chick survival is conditional on the hen surviving. Hen mortality during the breeding season was rare, and occurred primarily between the fall and following spring (September–March; Lyons 2017). Therefore, excluding these broods from analysis is unlikely to bias the results. We included broods where more than one hen flushed and we were able to discern distinct size classes among chicks and identify the appropriate size class for the focal hen ($n = 2$), but omitted one brood where we could not determine the focal hen for the chicks.

Model implementation

We used the package jagsUI (Kellner 2017) to fit the model in JAGS ver. 4.3.0 (Plummer 2017) using the program R ver. 3.5.0 (<www.r-project.org>). For our simulated data sets, we modeled survival and detection as a function of an intercept and a covariate. Both detection and survival were mapped to the appropriate scale using the logit link and we used logistic priors ($\mu = 0$, $\sigma = 1$) for all parameters (Supplementary material Appendix 3). We used logistic priors because they are less informative then traditional 'vague' priors on the probability scale (e.g. Normal($\mu = 0$, $\sigma^2 \geq 100$)) and improves MCMC mixing and convergence (Hooten and Hobbs 2015, Northrup and Gerber 2018).

We generated posterior estimates for detection probability, survival probability, and all covariate parameters from three chains of 50 000 iterations after a 1000 iteration adaptation phase. We discarded the first 10 000 samples and did not thin the remaining iterations (Link and Eaton 2012). We examined trace plots of ~10 simulations under each sample size and detection scenario for convergence and evaluated convergence of the remaining simulations when the Gelman–Rubin convergence diagnostic ($\hat{R}$, Gelman and Rubin 1992) <1.1. We evaluated model performance by calculating the difference between the posterior median and the data-generating value for each parameter for each simulation to assess whether parameters were calibrated (Little 2006). We also calculated the coverage of the 95% credible interval (CRI) and the range of the 95% CRI, as additional measures of model performance, and averaged these values among the 300 simulations within each scenario

We analyzed the pheasant brood survival data by modeling survival as a two-part process comprised of an intercept-only survival model and a binary variable indicating whether the hen experienced total brood loss. We modeled detection as a function two covariates (flush quality and Robel height). We determined a hen had experienced complete brood loss when we observed the absence of chick droppings at the roost site, the hen failing to return to the roost site within 15 min of a flush, or the hen renesting. We used logistic priors ($\mu = 0$, $\sigma = 1$) for all parameters. We performed a posterior predictive check using the Freeman–Tukey statistic (Conn et al. 2018) and estimated the overdispersion parameter ($\hat{c}$) to assess model fit.

We used R2OpenBUGS (Sturtz et al. 2005) to call OpenBUGS (Lunn et al. 2012) from within R ver. 3.5.0 to analyze our field data. We ran three parallel chains for 50 000 iterations and discarded the first 10 000 samples, retaining 1 in every 10 iterations. We calcuated the median posterior estimates of survival probability in each year, detection probability and covariate values for flush quality and Robel height, as well as the median brood size and difference in survival between years. We scaled Robel height measurements to a mean of zero and standard deviation of one prior to analysis and evaluated model convergence by examining the trace plots of parameter estimates and confirming all estimates of $\hat{R}$ were <1.1.

Results

Simulation study

Estimated posterior median parameter values were generally accurate and parameter error was most often <|0.05| for covariates of survival or detection, except when sample sizes were small or detection was low (Fig. 1a–d, Supplementary material Appendix 4 Table A4.1). Error in detection and estimates of survival was generally <|0.02|, and decreased with increasing sample sizes and detection probability (Fig. 1a–d, Supplementary material Appendix 4 Table A4.1). All parameters in all chains appeared to stabilize and all

95% CRIs contained the true values (Supplementary material Appendix 4 Table A4.1). CRIs were larger when detection and sample sizes were low (Supplementary material Appendix 4 Table A4.1). However, chains exhibited poor mixing and low effective sample sizes when detection was ≤0.4. We ran an additional 100 simulations using three visits ($n = 30$ broods, $p = 0.4$), which improved mixing and resulted in estimates of error that were equivalent to models with greater detection probability.

Error increased when we simulated data where survival between counts was not 1 (Fig. 3a–d, Supplementary material Appendix 4 Table A4.2). In these cases, error of the detection parameter tended to be negative while habitat and survival were positive. The magnitude of the increase in parameter error varied among specific combinations of DSR and observation period length (Fig. 3a–d, Supplementary material Appendix 4 Table A4.2). For example, when DSR was 0.99, there was no substantive difference in error among observation period length (0.022, 0.0210, 0.020; one, three and four days respectively), but was slightly larger compared to the model assuming perfect survival (0.01). Even when the daily survival rate was 0.97 and the time between counts was four days, the error in estimates of survival and detection (0.034, −0.047; respectively) were only slightly larger compared to when survival was assumed perfect (0.01, −0.01; Fig. 2a–d, Supplementary material Appendix 4 Table A4.2). All 95% CRIs contained the true value and there was no apparent increase in the width of 95% CRIs. However, when daily survival was ≤0.97 and the time between counts was three or four days, posteriors were poorly identified and chains exhibited slow mixing and small effective sample sizes.

Pheasant chick survival

Mean hatch size was not significantly different between years (2015: 11.2; 2016: 11.9). We observed four hens that experienced complete brood loss. Chick survival differed between years (0.12; 95% CRI: 0.074, 0.166). The estimated chick survival probability was 0.71 (95% CRI: 0.64, 0.79) in 2015 and 0.83 (95% CRI: 0.76, 0.91) in 2016. The estimated brood size at 15–22 days was 7.9 (95% CRI: 7.2, 8.9) chicks per brood in 2015 and 10.0 (95% CRI: 9.1, 11.0) in 2016. By contrast, naïve estimates of mean chick survival and brood size, which assume perfect detection, were 0.56 and 6.03, respectively. The estimated median detection probability for a chick was 0.56 (95% CRI: 0.50, 0.61), but increased with decreasing vegetation density at the flush locations ($\beta_{\text{Robel height}} = -0.23$; 95% CRI: −0.35, −0.10). The estimate of detection probability was significantly greater when observers believed they flushed a brood off a roost ($\beta_{\text{Flush quality}} = 3.31$; 95% CRI: 2.73, 3.94). Estimated detection probability was 0.91 when a flush was considered 'good' and 0.29 when a flush was considered 'poor' when holding vegetation density at its mean value. Under optimal conditions, when vegetation was ≤0.1 dm and the brood was flushed from their roost, estimated detection was as high as 0.94, but such instances were rare. The estimated Bayesian p-value calculated from the posterior predictive check was

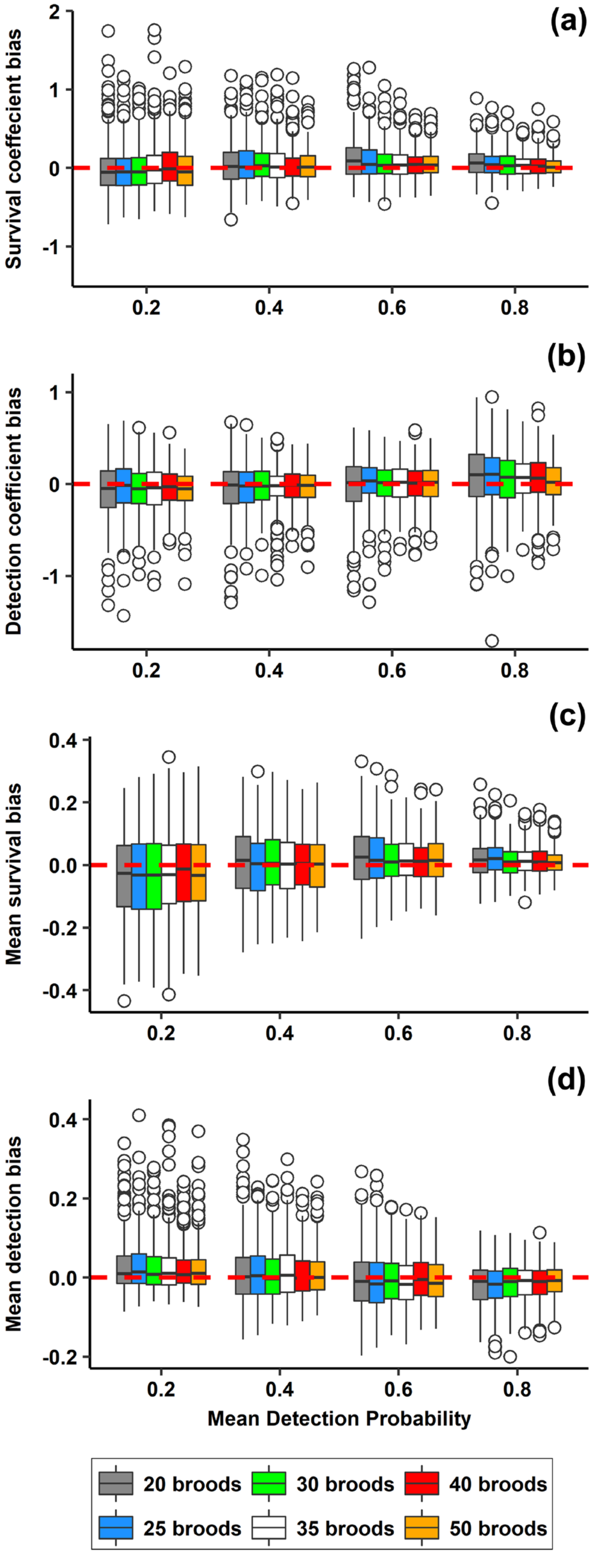

Figure 2. Boxplot of the difference between the median of the posterior for each parameter and data-generating values from 300 simulations under varying detection probabilities and sample sizes for (a) survival coefficient, (b) detection coefficient, (c) mean survival probability and (d) mean detection probability. The red dashed line indicates zero difference.

0.08 and the overdispersion parameter ($\hat{c}$) was 1.5, indicating the absence of major lack of fit (Conn et al. 2018).

Discussion

Intensive marking studies to estimate juvenile survival may be impractical due to limits of personnel, time, money, or concerns over animal welfare. Thus, models that estimate juvenile survival from repeated counts of unmarked offspring are a valuable alternative. Our application of common hierarchical models and an appropriate sampling method addresses shortcomings of existing approaches to estimating survival of unmarked young, such as the assumption of perfect detection, or poor model performance with small sample sizes. This simulation study demonstrated how a hierarchical modeling approach can produce properly calibrated estimates of survival over a range of sample sizes and detection probabilities with as few as two successive flush counts during a period when daily survival approximates 1. Like many models that account for imperfect detection, the error of estimates decreased and precision increased with increasing detection probability (Royle 2004, McCaffery et al. 2016). For instance, although two visits appeared to be sufficient to reach convergence when detection was extremely low (e.g. 0.2), estimates had extremely wide credible intervals, low effective sample sizes, and were poorly identified, which reduced their utility. However, with higher detection probabilities (>0.4) meaningful credible intervals (e.g. width <0.4) were attained with as few as 20 broods. Additionally, our approach allows for the estimation of covariates that may be influencing both survival and detection, which is often of ecological and management interest.

We were able to obtain informative estimates of pheasant chick survival using only two brood flushes from 38 broods. We were also able to identify several covariates that were important for detecting young pheasants. The estimated detection probability of a pheasant chick was 0.56 but increased to 0.91 under optimal conditions (i.e. a good flush and mean vegetation density) and may have been as high 0.94 when vegetation was ≤0.1 dm. Failing to account for imperfect detection in our study would have led to substantially biased estimates of chick survival and broods. Moreover the effect of habitat-related covariates on detection could have led to spurious conclusions about the relationship between habitat conditions and survival. Thus, accounting for imperfect detection should be incorporated into future studies using flush counts. Survival was also 12% greater in 2016 than 2015 which may have been attributable to the above average precipitation our study area received in 2015 (Illinois Region 5; Midwestern Regional Climate Center 2016) This is consistent with several other studies of chick survival in waterfowl and other precocial bird species (Pietz et al. 2003, Fondell et al. 2008, Brudney et al. 2013). In our study, the increased rainfall during 2015 may have led to higher rates of total brood failure (n = 3) than in 2016 (n = 1).

Though our tests of goodness-of-fit suggested minor lack of fit, we believe these results are still acceptable. Compared to other models with poorer fit, derived estimates of

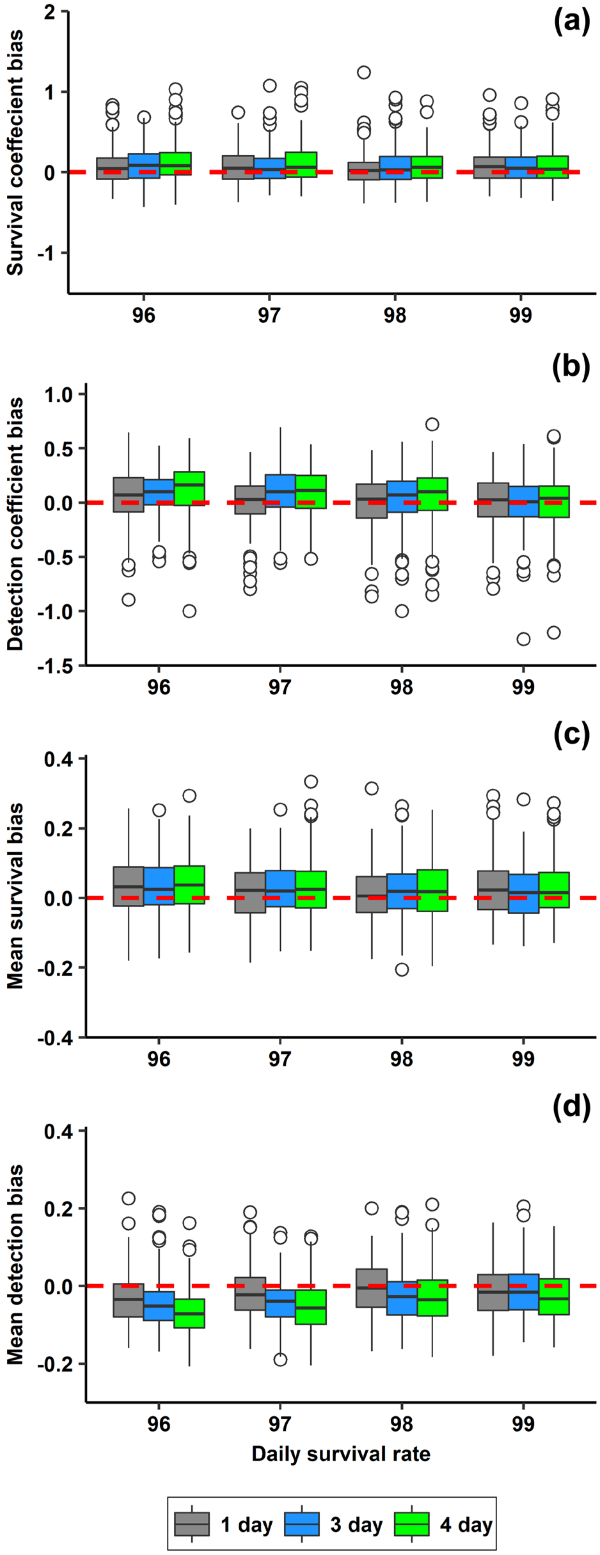

Figure 3. Boxplot of the difference between the median of the posterior for each parameter and data-generating values from 300 simulations when daily survival between flush counts was <1, and the amount of time between counts varied for (a) survival coefficient, (b) detection coefficient, (c) mean survival probability and (d) mean detection probability. The red dashed line indicates zero difference.

survival and brood size were generally the same. Additionally, our estimate of $\hat{c}$ (1.5) still falls within the range of values deemed to generally acceptable within the ecological literature (White and Burnham 1999). Though accounting for such extra-binomial variation in survival can be accomplished via an overdispersion parameter in the model, our sample sizes were too small to do so. The reality of small sample sizes associated with collecting data such as these may make highly parameterized models difficult to fit. Therefore, we encourage those who may use this approach to ensure as many broods as possible are counted at least twice, collecting as much data as possible, in order to support more parameterized, biologically plausible models.

The chick survival model we present relies on the assumptions of demographic closure between repeated counts and the assumption of no brood-mixing between hatching and surveys. While this assumption is certainly violated, our results demonstrate that estimates are robust, as long as the daily survival rate is near 1 (i.e. >0.98), conditions likely to have been observed in our field study. In 2015, all individuals from a small sample (n = 28) of all radio-marked pheasant chicks alive at seven days survived until ~15 days, the age when chicks molted and transmitters fell off (Lyons 2017). Furthermore, we found no systematic pattern of smaller counts on second flushes (Supplementary material Appendix 5 Fig. A5), which would be expected if numerous individuals were dying between flush counts. Daily survival of many species will approximate one after the first few weeks of life (Riley et al. 1998, Dreitz 2009, Davis et al. 2016) and even when daily survival is <1, error can be minimized by ensuring replicate counts are performed in close temporal proximity. The assumption of no brood mixing, on the other hand, may not be appropriate for some species. Brood mixing probabilities may be as high 21% among northern bobwhites (Faircloth et al. 2005) and greater sage grouse (Dahlgren et al. 2010), but can be as low as 4% among pheasants (Riley et al. 1998). Consequently, we recommend caution if trying to estimate chick survival for populations that experience high rates of brood amalgamation (Dahlgren et. al 2010), though the model could be modified to incorporate brood-mixing with appropriate data.

Like all models, this one has the potential for misuse that may lead to inaccurate estimates or inferences. However, these pitfalls can easily be addressed with careful study design. In general, the counts should be carried out on separate days, not as multiple-observer counts. Two counts are only a minimum, and more counts should be performed but are contingent on meeting assumptions of closure over a longer period and should consider whether additional counts are necessary as such disturbance could adversely influence behavior or survival. To ensure that chicks are available to be detected, observers should plan flush-counts when the parent and chicks are most likely to be in close proximity to each other, such as at a roost. Our experience led us to perform almost all our counts at dawn to ensure the chicks were with the hen and thus, likely to be flushed together.

Selecting the period to estimate survival may be subjective but should be based on biological reasoning where possible, and researchers should be aware of the limitations of their inference as a result. We were unable to flush pheasant chicks before 15 days because they are only capable of weak flight and the dense vegetation of grasslands prevented us from counting chicks as they ran. Similarly, most attempts to flush broods at ~40 days failed because broods often ran away as we approached. Our choice of estimating survival to 15–22 days was based on biological reasons as well as the aforementioned logistical constraints. Though survival of many precocial birds, is lowest during the few days post-hatch before reaching a relatively high level (Pietz et al. 2003, Dreitz et al. 2009, Davis et al. 2016), we encourage those attempting to use this approach to minimize the range of brood ages over which counts are made to minimize any potential bias due to variable exposure periods. While estimates obtained using this approach are not representative of survival to independence, they can provide insight about the environmental factors that lead to mortality for the majority of chicks. This framework can also be expanded to accommodate additional visits and observation periods, when practical (Fig. 1), permitting the estimation of survival over longer periods of time.

Despite the potential limitations, estimating chick survival using the framework we present offers flexibility that can address the problems related to the violation of assumptions provided sufficient data exist. We attempted to reparameterize the model to account for survival <1 during repeated counts, but the error for all parameter estimates were large with only counts of unmarked chicks. Incorporating additional sources of data could improve these estimates. Brood mixing could be explicitly modeled as the emigration parameter in a robust-design framework (Pollock 1982), or implicitly as apparent survival and gains in an open meta-population model (Dail and Madsen 2011). Still, the increasing complexity of the model would require larger sample sizes and additional sources of data beyond simple counts, which may limit the utility of such a model in practice (Dail and Madsen 2011). Researchers could use field evidence (e.g. observing chicks of multiple age classes) to estimate both the probability of brood-mixing and the number of adopted young, which could be incorporated into a more complex model as informative priors (Morris et al. 2015) or as an additional data source. Multiple types of data can easily be incorporated into hierarchical models (Powell et al. 2000, Schaub et al. 2007, Linden and Roloff 2015), such as small sample of radio-marked individuals or capture-recapture data, to estimate daily survival or emigration (brood mixing) parameters. Finally, the hierarchical Bayesian framework can be easily parameterized to estimate several different derived parameters including the total number of chicks, mean brood size and average daily survival.

With the exception of a few, well studied, taxa, there are limited number of published estimates of survival for juvenile animals. The model and approach we present complements existing methods by addressing important issues such as imperfect detection and poor performance with large group sizes, but is more resource and time efficient compared to mark–recapture studies and other brood count methods. The approach we present performs reasonably well with small sample sizes, though more than two visits during a period when daily survival approaches one may be necessary when detection is ≤0.4. It is also important that users identify useful covariates for the detection and survival process. The double-binomial structure of this model means that posterior distributions of parameters from models without covariates, on at minimum the detection process, may be not be uniquely identified (D. Tyre unpubl.). Most importantly, our approach provides a flexible foundation to address a variety of real-world challenges and will be a useful tool for wildlife managers and researchers seeking to make informed management decisions.

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Supplementary material (available online as Appendix wlb-00529 at <www.wildlifebiology.org/appendix/wlb-00529>). Appendix 1–5.