

# A Bayesian multinomial logistic exposure model for estimating probabilities of competing sources of nest failure

ABIGAIL J. DARRAH,<sup>1,2\*</sup>  JONATHAN B. COHEN<sup>1</sup> & PAUL M. CASTELLI<sup>3</sup>

<sup>1</sup>Department of Environment and Forest Biology, State University of New York – College of Environmental Science and Forestry, 1 Forestry Drive, Syracuse, NY 13210, USA

<sup>2</sup>Audubon Mississippi Coastal Bird Stewardship Program, 5009 Main Street, Moss Point, MS 39563, USA

<sup>3</sup>US Fish and Wildlife Service, Edwin B. Forsythe National Wildlife Refuge, 800 Great Creek Road, Galloway, NJ 08205, USA

Understanding causes of nest loss is critical for the management of endangered bird populations. Available methods for estimating nest loss probabilities to competing sources do not allow for random effects and covariation among sources, and there are few data simulation methods or goodness-of-fit (GOF) tests for such models. We developed a Bayesian multinomial extension of the widely used logistic exposure (LE) nest survival model which can incorporate multiple random effects and fixed-effect covariates for each nest loss category. We investigated the performance of this model and the accompanying GOF test by analysing simulated nest fate datasets with and without age-biased discovery probability, and by comparing the estimates with those of traditional fixed-effects estimators. We then exemplify the use of the multinomial LE model and GOF test by analysing Piping Plover *Charadrius melodius* nest fate data ( $n = 443$ ) to explore the effects of wire cages (exclosures) constructed around nests, which are used to protect nests from predation but can lead to increased nest abandonment rates. Mean parameter estimates of the random-effects multinomial LE model were all within 1 sd of the true values used to simulate the datasets. Age-biased discovery probability did not result in biased parameter estimates. Traditional fixed-effects models provided estimates with a high bias of up to 43% with a mean of 71% smaller standard deviations. The GOF test identified models that were a poor fit to the simulated data. For the Piping Plover dataset, the fixed-effects model was less well-supported than the random-effects model and underestimated the risk of exclosure use by 16%. The random-effects model estimated a range of 1–6% probability of abandonment for nests not protected by exclosures across sites and 5–41% probability of abandonment for nests with exclosures, suggesting that the magnitude of exclosure-related abandonment is site-specific. Our results demonstrate that unmodelled heterogeneity can result in biased estimates potentially leading to incorrect management recommendations. The Bayesian multinomial LE model offers a flexible method of incorporating random effects into an analysis of nest failure and is robust to age-biased nest discovery probability. This model can be generalized to other staggered-entry, time-to-hazard situations.

**Keywords:** competing risks, exclosures, goodness-of-fit test, nest abandonment, nest predation, nest survival, Piping Plover.

Quantifying avian nest success is a common objective of many field studies with such wide-ranging themes as the evolution of life history patterns

(Martin 1995), source-sink dynamics (Lloyd *et al.* 2005), effects of land use on avian communities (Twedt *et al.* 2010) and management of harvested or endangered species (Stephens *et al.* 2005, Cohen *et al.* 2009, Guereña *et al.* 2016). Nest success, i.e. the probability that a given nest attempt

\*Corresponding author.

Email: glyphorynchus@gmail.com

produces at least one hatchling (precocial species) or fledgling (altricial species), is a critical component of productivity (Hoekman *et al.* 2002), and is more easily observed and measured than fledging, recruitment or annual survival rates; it is also generally easier to increase nest survival probability through management actions than it is to increase other vital rates (e.g. van der Burg & Tyre 2011, Wilson *et al.* 2012). Thus understanding environmental and management effects on nest success and on different causes of nest failure are particularly relevant to the conservation of threatened and endangered bird species.

Most nest survival models recognize two nest fates, survival and failure, the latter of which may include failure from multiple causes, such as predation, abandonment, parasitism and weather (Ricklefs 1969). Few models have been developed to estimate separately the rates of failure due to different causes, although understanding the factors that lead to different types of nest failure can be of management interest. For example, abandonment at Piping Plover *Charadrius melodus* nests with wire exclosures (Melvin *et al.* 1992) has been shown to be indicative of adult mortality due to predators targeting incubating adults as they leave exclosures (Murphy *et al.* 2003, Barber *et al.* 2010, Roche *et al.* 2010) and thus has different demographic consequences than other nest failure types and may offset the benefits of increased hatching rates at exclosed nests (Calvert & Taylor 2011). In such a context, modelling nest survival alone as a function of exclosure use is not sufficient to predict population-level consequences; more generally, if a covariate has opposing effects on different types of nest failure, then its importance can only be revealed through a multi-fate study (Etterson *et al.* 2007a). To date, the best available method for modelling multiple sources of nest failure is the Etterson *et al.* (2007b) multinomial extension of their original Markov chain nest survival model (Etterson & Bennett 2005). This model has the capacity to include nest- and time-varying covariates and estimates of nest fate classification error, and can be analysed using maximum-likelihood methods with the software package MCESTIMATE (Etterson 2013). The primary drawbacks of the model are: (1) the classification error parameters are not estimable without establishing evidence-based estimates from field studies using known-fate nests (Etterson & Stanley 2008); (2) large numbers of

parameters can result in unstable maximum-likelihood estimates in survival models (Cao & He 2005); and (3) the model does not currently allow for inclusion of random effects. The use of a Bayesian approach offers a solution to the second and third points.

Random effects modelling is generally appropriate when covariate levels represent a random draw from a larger population, where the goal is to extend inference beyond the levels (e.g. sites) used in the study (Kéry & Schaub 2012), and is a convenient means of accounting for unknown sources of heterogeneity that can bias survival estimates (Natarajan & McCulloch 1999, Stephens *et al.* 2005). Few nest survival models analysed in a frequentist framework are capable of incorporating random effects, largely due to computational limitations (Rotella *et al.* 2004). PROGRAM MARK can incorporate simple random effects models into survival analyses (Cooch & White 2017). The Stephens *et al.* (2005) model can incorporate a single site-level random effect but not multiple random effects or finer heterogeneity sources such as nest or pair identity. Additionally, Heisey *et al.* (2007) caution against the use of random effects in left-truncated datasets such as are typical for nest survival studies, due to the potential for age-biased discovery probability and the possibility that entire 'clusters' will be lost before discovery, resulting in nest survival estimates with a high bias. However, little attention has been devoted to examining this problem. With ever-increasing computer processing speed and the introduction of user-friendly programs such as WINBUGS (Lunn *et al.* 2000) and JAGS (Plummer 2013), Bayesian methods have now become more accessible and more widely used in ecology, providing a flexible means of incorporating random effects into nest survival analysis and assessing the performance of such models with simulated data.

Testing the fit of nest survival models presents several difficulties, and such tests are not available in most software packages and instead must be custom-built (Dinsmore *et al.* 2002, Rotella *et al.* 2004, Shaffer & Thompson 2007). Shaffer and Thompson (2007) discussed the inappropriateness of Chi-square tests given the small sample sizes among ages typical of most nest survival studies and present an *ad hoc* graphical method for assessing the fit of age-specific nest survival models. Sturdivant *et al.* (2007) described a kernel-smoothed residual statistic for testing the

goodness-of-fit for nest survival models with random effects. Schmidt *et al.* (2010) used a deviance statistic calculated from the cumulative survival curve in a Bayesian analysis of a model for nest and chick survival. Of these, only Sturdivant *et al.* (2007) used data simulation to assess the ability of the fit test to correctly reject inappropriate models. For a multinomial analysis of nest fate, the software MCESTIMATE provides several different types of goodness-of-fit tests (Etterson 2013), including a multinomial extension of the Hosmer–Lemeshow test (Hosmer *et al.* 2013).

In this paper we develop a multinomial extension of the logistic exposure nest survival model (Shaffer 2004), analysed in a Bayesian framework for the purpose of incorporating multiple random effects. Our objectives are to: (1) describe the model; (2) use simulation to demonstrate the ability of the model to provide unbiased estimates of fixed effects and hyperparameters governing the random effects; (3) assess how the random-effects model performs in cases of age-biased discovery probability; (4) demonstrate that omitting site-level random effects can lead to biased parameter estimates and underestimated parameter variances; (5) describe and evaluate the performance of a goodness-of-fit test for this model; and (6) use the model to analyse an example dataset from a study of Piping Plovers from the US Atlantic Coast. Our method provides a flexible and generalizable framework for analysis of factors affecting nest fate that can be expanded to include other types of ragged-entry multinomial survival or cumulative hazard data.

## METHODS

### Field data collection

Biologists overseeing 46 management units ('sites') in eight states (Maine, New Hampshire, Massachusetts, Rhode Island, New York, New Jersey, Virginia and North Carolina) collected Piping Plover nest fate data on 443 nests in 2015 using a standardized protocol. Site managers erected wire cages (exclosures) at 175 nests among all sites, typically within 5 days of clutch completion. Participants checked Piping Plover nests at intervals typically ranging between 1 and 5 days and recorded the date the exclosure was erected (exclosed), visually estimated the per cent vegetation cover within 2 m of the nest, and categorized the

surrounding beach zone as overwash, dune or berm. Vegetation cover did not change throughout the active period of most nests, but for the few that experienced vegetation growth, vegetation cover for each interval was calculated as the average of the cover recorded during the first and second visits. At each visit, observers classified the nest as active, hatched, abandoned, predated, flooded or other/unknown, based on a common set of criteria for assigning nest fate. Abandonment was determined by the presence of eggs combined with a lack of fresh Plover tracks, lack of parental presence during at least two consecutive nest checks, and was at some sites verified by tipping the eggs on end; if the eggs were still tipped after 1 day this indicated lack of parental attendance. Observers determined the ages of nests whenever possible based on the number of eggs present in a clutch if the nest was found during the laying phase (where day 0 = day first egg was laid), by back-dating successful nests assuming hatch occurred on day 34 (Cairns 1982) or via egg-floating (Liebezeit *et al.* 2007).

### Model description

For illustration we discuss a model in which there are three sources of nest loss. Our case study involves a precocial species (Piping Plover) but this model can be used without modification for altricial species. This model has the form:

$$y_{ij} \sim \text{multinomial} \left( \left[ P_s(t)_{ij}, P_d(t)_{ij}, P_o(t)_{ij}, P_a(t)_{ij} \right], 1 \right) \quad (1)$$

where  $y_{ij}$  are the observed fates of nest  $i$  at nest-specific interval  $j$ , where each interval is  $t$  days long, and observed nest fates are survival ( $s$ ), predation ( $d$ ), flooding ( $o$ ) or abandonment ( $a$ ). The  $y_{ij}$  follow a multinomial distribution with one trial per nest check interval, where the  $P_{F_{ij}}$  are the probabilities of the nest being at fate  $F$  ( $F = \{s, d, o, a\}$ ) by the end of a check interval  $j$ , given the interval length  $t$ . Nest fate is assumed to be classified correctly. Nests of unknown fate can be accommodated in the model by assigning NA (not applicable) to the terminal  $y_{ij}$  for such nests; this will inflate the variance of the parameter estimates to reflect the uncertainty. Nests are assumed to survive or fail due to cause  $l$  ( $l = \{d, o, a\}$ ) independently of one another.

The effects of covariates on nest loss probability during interval  $j$  are modelled as linear predictors of the form:

$$\eta_{lij} = \beta_{lc}X_{ij} + \gamma_{lr}, \gamma_{lr} \sim N_l(\mu, \Sigma) \quad (2)$$

where  $\beta_{lc}$  is a matrix of regression coefficients for each covariate  $c$  associated with nest loss type  $l$ , and  $X_{ij}$  is the design matrix with nest- and interval-specific covariate values. The  $\gamma_{lr}$  represent random effects of site  $r$  for loss type  $l$ , which are assumed to follow a multivariate normal distribution with a mean vector ( $\mu$ ) of zeroes and variance-covariance matrix  $\Sigma$ . Daily nest fate probabilities for nest  $i$  in interval  $j$  ( $p_{Fij}$ ) follow the standard multinomial logit function with survival probability as the reference category:

$$p_{sij} = \frac{1}{1 + \sum e^{\eta_{lij}}} \quad (3)$$

and daily nest loss probabilities for each loss category  $l$ :

$$p_{lij} = \frac{e^{\eta_{lij}}}{1 + \sum e^{\eta_{lij}}} \quad (4)$$

For intervals of length  $t$ , survival probability is  $P_{sij} = (p_{sij})^t$  and nest loss probabilities are the sum of the daily probabilities of surviving and then succumbing to loss  $l$  on any particular day during interval  $t$  (Heisey & Fuller 1985):

$$P_{lij} = \frac{p_{lij}}{1 - p_{sij}} \times (1 - (p_{sij})^t) \quad (5)$$

For example, for a nest check interval of 3 days, if the daily survival probability is 0.8 and daily predation probability is 0.1, then the probability of predation during the 3-day interval is the sum of the probabilities of being predated on day 1 + the probability of surviving day 1 and being predated on day 2 + the probability of surviving to days 1 and 2 and being predated on day 3, which is  $0.1 + 0.8 \times 0.1 + 0.8 \times 0.8 \times 0.1 = (0.1/(1 - 0.8)) \times (1 - 0.8^3) = 0.244$ . In this formulation, daily nest fate probabilities are assumed to be equal for each day during nest check interval  $j$ , unless daily time-varying covariates are incorporated. Although we do not provide an example in this article, this model can be reformulated to a multinomial version of the logistic exposure model described in Schmidt *et al.* (2010) to explicitly

incorporate covariates for each day within a nest check interval.

In all analyses using this model, we used Markov chain Monte Carlo (MCMC) simulation as implemented in JAGS 3.4.0 (Plummer 2013), taken from program R 3.3.1 (R Core Team 2016) via the package *jagsUI* (Kellner 2015). We ran three chains with a thinning rate of one and assessed chain convergence by visually inspecting the trace plots and using the Gelman–Rubin diagnostic ( $\hat{R}$ ; Gelman *et al.* 2004) and considered convergence to be achieved at  $\hat{R} < 1.05$  for all parameters. We chose non-informative wide priors for all parameters: for variance hyperparameters, we used a uniform distribution of 0–50, and for all intercepts and fixed-effect covariates we used a normal distribution with mean zero and precision 0.001.

### Data simulation to assess model performance

To examine the ability of this model to provide unbiased parameter estimates, we conducted two exercises using repeated simulation of nest survival datasets (Simulations A and B) followed by analysis of those datasets using our model. In both exercises, we repeated 1000 simulations of nest fate datasets of  $n = 1000$  nests scattered among 40 sites. Simulated nests began entering the study beginning at day 1 of the season, with initiation dates randomly drawn from a binomial distribution of size 120 with mean set to 32 days after the start of the season. Nests were discovered and subsequently observed with a daily discovery probability of 97% regardless of age, multiplied by a daily nest check probability of 50%. In all cases, some proportion of nests that were initiated were never discovered, such that the ending sample size for each simulation averaged  $n = 855$  nests. In Simulation A, we simulated data using one set of intercept values and random effect hyperparameters, with zero covariance among random effects, and analysed each dataset using an intercept-only model with site-level random effects. Each MCMC chain was set to 10 000 iterations with a burn-in of 5000. For Simulation B, we removed the random effects and added two fixed-effect covariates each to the predation and abandonment linear predictors (simulation code in Appendix S1). Enclosure was a binomial covariate varying by nest and time that decreased predation and increased abandonment probability, vegetation was a nest-level



binomial covariate that reduced predation, and nest initiation date was a discrete normal nest-level covariate that decreased abandonment probability. For each simulation, 50% of nests were randomly selected to receive exclosures, which were then randomly assigned to receive the exclosure at an age of between 4 and 8 days, roughly reflecting variation in real management practices and logistics. Sixteen per cent of nests were randomly assigned large values for vegetative cover. We analysed each of the 1000 simulated datasets (analysis code in Appendix S2) with a fixed-effects model with all covariates that were used to simulate the data, with chain lengths of 5000 and a burn-in of 2000.

### Random effects in the presence of age-biased discovery

To test the effect of age-biased nest discovery on the performance of random-effects models, we conducted a third simulation (Simulation C) using 1000 simulations of  $n = 1000$  nests each. We simulated nest fate data with a random site effect on predation probability and no covariates, and we set nest discovery probability for a hypothetical altricial species to 30% for nests aged 0–10 days, 50% for 11–20 days and 90% for 20–34 days because nests are more easily discovered in the incubation than in the building stage (Smith *et al.* 2009), and for altricial birds, discovery probability is greatest during the nestling stage due to frequent parental trips to the nest (Russell *et al.* 2009). We estimated the predation intercept and variance hyperparameter for each dataset using chain lengths of 6000 and a burn-in of 3000, and compared these parameter estimates with the true values and to the parameters estimated from the first simulation exercise.

### Effects of using the 'wrong' model for inference

We used a fourth simulation exercise (Simulation D) to demonstrate the effects of estimating parameters using a fixed-effects model when the true model underlying the data contains site-level random effects. We simulated 100 datasets of  $n = 400$  nests each using random site effects for each fate, and with fixed exclosure effects on predation and abandonment probabilities. Each dataset was analysed with both the 'correct' model

(i.e. all random site effects and fixed covariates) and the 'wrong' model (fixed effects only). To assess the performance of each model, we estimated the mean bias between the estimated and true parameter values and compared the magnitude of parameter standard deviations between models.

### Piping Plover data analysis

To analyse the Piping Plover nest fate data, we constructed a model with uncorrelated random site effects for all nest failure categories, exclosure as a covariate for predation and abandonment probability, vegetation cover (0%, 1–20%, > 20%) as a covariate for predation, and nest initiation date and beach zone (berm, dune, overwash) as covariates for abandonment. We scaled all continuous covariates to have a mean of zero and a standard deviation of one and conducted Bayesian model selection using the indicator variable approach (Kuo & Mallick 1998, Link & Barker 2006), where each regression parameter  $k$  is multiplied by an indicator variable  $w_k$  that follows a Bernoulli distribution with a prior probability of 0.5. Using this approach, during each MCMC sample the indicator variables were given a value of one if the covariate occurred in the model and zero otherwise. We used the estimated  $w_k$  to calculate the Bayes' factor (BF) for each covariate, where the BF represents the odds ratio of inclusion (Smith *et al.* 2011). Following the recommendations of Link and Barker (2006, p. 2632) and the example of Converse *et al.* (2013), to maintain constant total model variance regardless of the number of parameters entering the model, we scaled the prior variances for each of the fixed-effect covariates by dividing the prior variance by the number of covariates entering the model at each iteration, with a gamma-distributed prior with parameters 3.29 and 7.8 assigned to the total model variance (R and BUGS code in Appendix S3). We ran three parallel chains with 70 000 iterations with a burn-in of 40 000.

### Goodness-of-fit assessment

To assess the goodness-of-fit (GOF) of our model, we used a modification of the GOF method described in Schmidt *et al.* (2010), extended to a multinomial framework and accounting for nests entering the study at different ages rather than

extrapolating the fate history backwards to initiation. During each MCMC iteration we simulated replicate fate observations for each nest under the observed nest check intervals and covariates in the model, with each nest set to hatch if it reached age 34 (R and BUGS code in Appendix S4). We computed separate fit statistics for each fate by comparing the observed fate history and expected cumulative fate probabilities (*sensu* Schmidt *et al.* 2010, p. 382). For each fate we used the fit statistic:

$$D_F = \sum_{ij} \frac{(F_{ij} - \phi_{F_{ij}})^2}{\phi_{F_{ij}}(1 - \phi_{F_{ij}})} \quad (6)$$

where  $\phi_{F_{ij}}$  are the probabilities of nest  $i$  surviving to nest check interval  $j - 1$  and being in fate  $F$  at the end of interval  $j$ .  $F_{ij}$  takes values of zero or one for each fate, with one indicating the nest was observed in fate  $F$ . Equation 6 is a modification of the fit statistic for multinomial regression given in Hosmer *et al.* (2013, p. 284); where they use expected observations in their fit statistic, we use cumulative probability curves in the denominator of Equation 6 because nests cannot return to any other fate after failure or hatch. We compared the  $D_F$  calculated using the observed data with those calculated using the replicate data to calculate the Bayesian  $P$ -value ( $Bp$ ) separately for each fit statistic, which represents the frequency that the observed statistics are greater than the replicated statistics. Values close to 0.5 indicate good fit, while values approaching zero or one indicate lack of fit (Gelman *et al.* 1996). To perform the GOF test on the real dataset, we used the subset of the data with known fates and known ages.

We investigated the performance of this GOF test by first using it to test the fit of nest fate data with the same model used to generate the data, and then by testing the fits of two incorrect models. We simulated a dataset of 1000 nests from 40 sites using the site variances, exclosure effects, nest initiation effect and vegetation effect parameters estimated from the real dataset. We tested the GOF of a model with all parameters used to generate the data (correct model), an intercept-only model and a model with fixed effects only (incorrect models). If this GOF test is an appropriate means of detecting lack of fit, then we expect the  $Bp$  values for the correct model to be close to 0.5 and the  $Bp$  values for the incorrect models to be close to zero or one.

We estimated the fit of the top Piping Plover model by incorporating the GOF test into a model including the random effects and all covariates with a  $BF > 1$ . To compare inferences and fit of models lacking random effects, we also analysed the Piping Plover data using a fixed-effects model including the same slope covariates, and an intercept-only model. We compared the parameter estimates, standard deviations and fit assessments of these models with those of the random-effects model.

## RESULTS

### Model performance

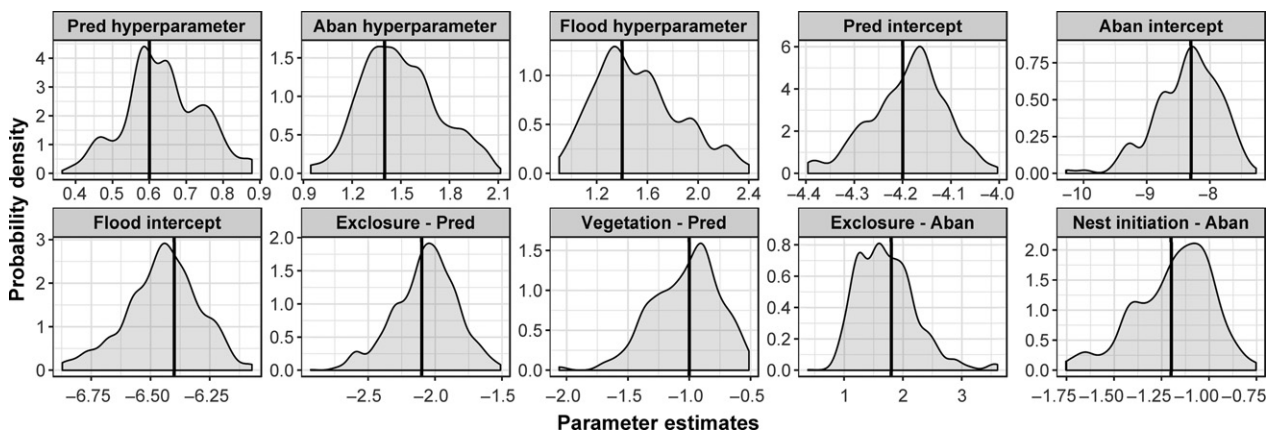
Both the random-effects (Simulation A) and the fixed-effects (Simulation B) models successfully estimated the variance hyperparameters and fixed covariates, with mean estimated values all within 5% of the true values used to simulate the datasets (Fig. 1).

### Random effects in the presence of age-biased discovery

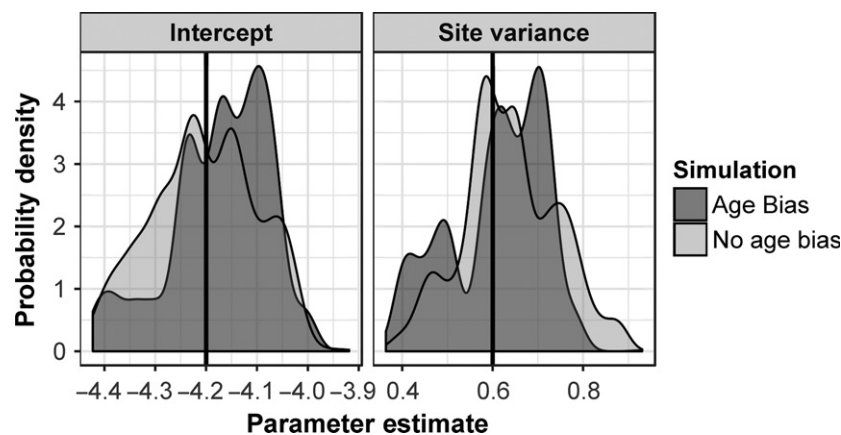
For the random-effects model analysis of data simulated with age-biased nest discovery probability (Simulation C), estimated values were within 5% of the true values and broadly overlapped the estimates from data simulated with constant discovery probability (Fig. 2).

### Effects of using the 'wrong' model for inference

For data generated using site random effects and analysed using multiple models (Simulation D), average bias for all parameters estimated using the correct random-effects model was 1.5%, with bias  $< 5\%$  for all parameters except for exclosure effect on abandonment (bias =  $-15\%$ ; Fig. 3). For estimates using the fixed-effects-only model, bias averaged 13% and was  $< 5\%$  only for the predation intercept and slope; bias was 10% for the flooding intercept, 12% for the abandonment intercept and  $-43\%$  for exclosure effect on abandonment (Fig. 3). Standard deviation estimates of the parameters averaged 71% smaller using the fixed effects model than the random effects model, ranging from 2% smaller for the predation intercept and slope to 64% lower for the flooding intercept (Fig. 4).



**Figure 1.** Posterior estimates from two sets (A and B) of nest fate simulations, each set containing 1000 simulated datasets ( $n = 1000$  nests each) and the true values (dark vertical lines) used to generate the datasets. Hyperparameters are from the random-effects models in Simulation A, and the remaining parameters are from the fixed-effects models in Simulation B. Intercepts and slopes are from the linear predictors of three nest failure categories: predation (Pred), abandonment (Aban) and flooding (Flood). Exclosure is the effect of nest exclosure use on predation and abandonment probabilities, vegetation is the effect of nest vegetation cover on nest predation and nest initiation is the effect of nest initiation date on abandonment probability.



**Figure 2.** Intercept and site variance hyperparameter values for daily probability of predation, estimated from two sets of 1000 nest fate datasets ( $n = 1000$  nests each) simulated using no detection bias (Simulation A) or with positive age-biased nest discovery probabilities (Simulation C), and the true values (dark vertical lines) used to generate the datasets.

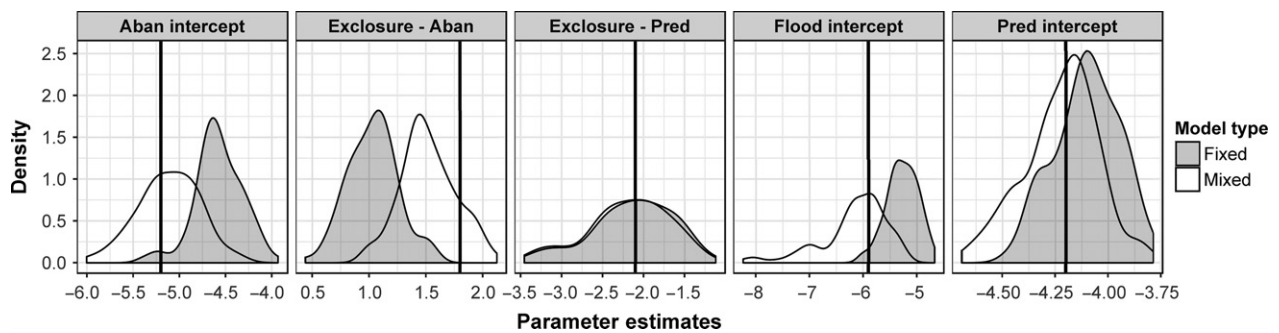
### Piping Plover nest fate analysis

The effects of exclosure use and nest initiation date on nest fate were well supported ( $w_k \geq 0.95$ ) by the model selection procedure, whereas vegetation cover and beach zone received low support, and with the 95% credible interval for beach zone overlapping zero (Table 1). Exclosure use reduced predation probability and increased abandonment probability (Fig. 5), and abandonment probability was negatively correlated with nest initiation date

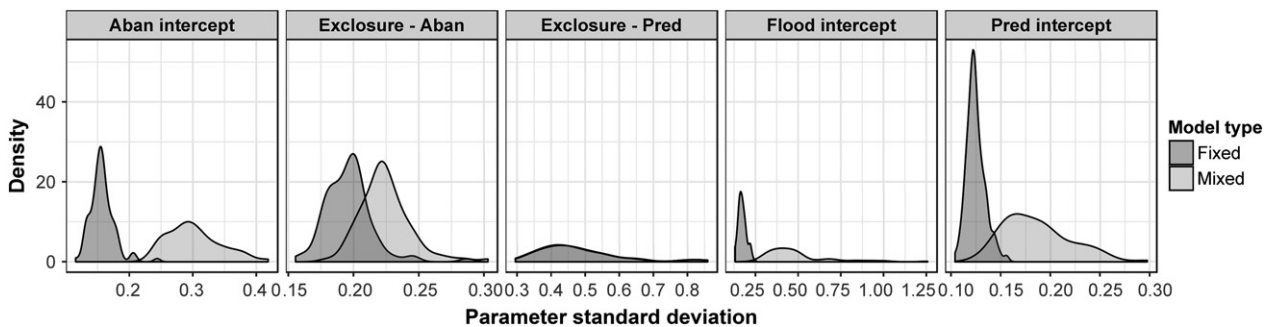
(Table 1, Fig. S1). Nests with > 20% vegetation cover had lower predation probability than nests with little or no vegetation (Fig. S2). The estimated among-site variances for flooding and abandonment probabilities were greater than that for predation probability (Table 1).

### Goodness-of-fit assessment

For data simulated using covariates and site random effects, the GOF test of the true model



**Figure 3.** Posterior parameter estimates for daily probability of predation (Pred), abandonment (Aban) and flooding (Flood) from 100 nest fate datasets ( $n = 400$  nests) simulated with site random effects, each analysed using a mixed-effects and fixed-effects model (Simulation D). Intercepts for each fate are shown as well as the regression coefficient for nest protection via enclosure use (Exclosure) on abandonment and predation probabilities. The true values used to generate the datasets are shown as dark vertical lines.



**Figure 4.** Posterior estimates of parameter standard deviations for daily probability of predation (Pred), abandonment (Aban) and flooding (Flood) from mixed-effects and fixed-effects models used to analyse 100 nest fate datasets ( $n = 400$  nests) simulated with site random effects (Simulation D). Intercepts for each fate are shown as well as the slope effect of nest protection via enclosure use (Exclosure) on abandonment and predation probabilities.

indicated a good fit ( $Bp_{\text{survival}} = 0.71$ ,  $Bp_{\text{abandonment}} = 0.40$ ,  $Bp_{\text{predation}} = 0.81$ ,  $Bp_{\text{flooding}} = 0.28$ ). The GOF test of the intercept-only model identified a lack of fit for all fates except flooding (which did not include fixed effect covariates in the simulation;  $Bp_{\text{survival}} = 0.99$ ,  $Bp_{\text{abandonment}} = 0.06$ ,  $Bp_{\text{predation}} = 1.00$ ,  $Bp_{\text{flooding}} = 0.46$ ). The GOF test of the fixed-effects-only model suggested a lack of fit for survival and predation probabilities ( $Bp_{\text{survival}} = 0.93$ ,  $Bp_{\text{abandonment}} = 0.31$ ,  $Bp_{\text{predation}} = 0.94$ ,  $Bp_{\text{flooding}} = 0.48$ ).

The GOF test indicated good fit of the Piping Plover model with site random effects and the top five covariate effects, whereas it indicated poor fit of the fixed-effects and intercept-only models, as evidenced by at least one  $Bp$  value  $> 0.95$  (Table 2). Parameter estimates of the fixed-effects and intercept-only models were of lesser magnitude for most covariates, such that despite the decreased variance around the estimates, the 95%

Bayesian credible interval for enclosure effect on abandonment overlapped zero in the fixed-effects model (Table 2).

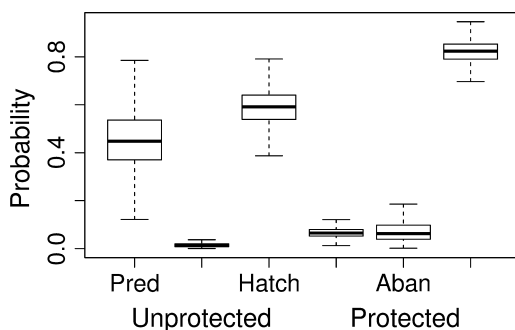
## DISCUSSION

This extension of the multinomial logistic exposure model makes it possible to estimate probabilities of different types of nest failures and serves as an unbiased estimator of failure probabilities, random effects variance and covariate effects even in the presence of age-biased detection probability, as evidenced by the simulation exercises. This model offers a flexible means of incorporating multiple and potentially correlated random effects, which can be important for providing unbiased estimates of fixed effects or can be of biological interest in their own right. For example, Link *et al.* (2002) used a model with correlated individual random effects in a model of annual survival and breeding



**Table 1.** Standardized parameter estimates, 95% Bayesian credible intervals (BCI), inclusion probabilities (weight) and Bayes' factors (BF) for variables hypothesized to affect daily probabilities of flooding, abandonment and predation of Piping Plover *Charadrius melodus* nests ( $n = 443$ ) at 46 sites along the US Atlantic Coast in 2015.

Parameter	Mean	Lower 95% BCI	Upper 95% BCI	Weight	BF
<b>Intercepts</b>					
Abandonment	-7.23	-8.67	-6.32		
Predation	-5.15	-5.64	-4.74		
Flooding	-6.47	-7.75	-5.65		
<b>Among-site variances</b>					
Abandonment	1.40	0.47	2.6		
Predation	0.62	0.24	1.12		
Flooding	1.39	0.73	2.52		
<b>Fixed effects on predation</b>					
Exclosure	-0.97	-1.36	-0.61	1.00	Inf
0–20% vegetation	-0.004	-0.24	0.22	0.64	1.78
> 20% vegetation	-0.40	-0.72	-0.11	0.64	1.78
<b>Fixed effects on abandonment</b>					
Exclosure	0.78	0.22	1.43	0.95	19
Nest initiation date	-0.99	-1.63	-0.44	0.99	99
Overwash	-0.20	-0.94	0.44	0.45	0.82
Dune	0.38	-0.06	0.83	0.45	0.82



**Figure 5.** Estimated 34-day interval probability of predation (Pred), abandonment (Aban) or hatch for Piping Plover (*Charadrius melodus*) nests with and without predator exclosures at 46 sites along the US Atlantic Coast in 2015. Boxes represent 25–75% interquartile ranges (IQR), lines represent medians, and whiskers represent data range excluding outliers ( $> 1.5$  times IQR).

probabilities of Black-legged Kittiwakes *Rissa tridactyla* to elucidate the life-history trade-offs between reproductive effort and longevity. Most often, random effects are included in models as a means of addressing potential sources of lack of independence. In our case, nests clustered by site

might be more likely to experience similar fates due to complex environmental factors, not all of which can be measured or incorporated into the model as fixed effects.

We demonstrated that if the underlying data contain un-modelled heterogeneity in the form of site random effects, traditional fixed-effects models can underestimate fixed-effects parameters and parameter variances, potentially affecting inferences. In our simulation example, the fixed-effects model underestimated the tendency of exclosure use to increase nest abandonment probability (indicative of adult mortality) and overestimated the probability of abandonment at unprotected nests. In a management context these discrepancies could result in overly liberal use of nest exclosures by underestimating their negative impacts on breeding adults. Parameter bias was negligible, on the other hand, for the predation intercept and exclosure effect, probably reflecting the fact that predation was the most common source of nest failure, thus providing enough data from all sites to estimate the overall mean parameters for predation adequately. Other studies have demonstrated biases in survival estimates (Natarajan & McCulloch 1999) and estimates of covariate effects (Stephens *et al.* 2005) in the results of fixed-effects analyses compared with mixed-effects models.

There has been concern that including random effects in left-truncated data could result in overestimating survival probability because the most 'frail' clusters might fail before discovery (Heisey *et al.* 2007). However, our simulations using constant daily nest discovery probability and age-biased discovery probability resulted in nearly identical, and unbiased, estimates of mean and site variance in predation probability. We suggest, as do Schmidt *et al.* (2010), that using site-level random effects may be less likely to result in missing entire frailty clusters compared with finer-level random effects such as individuals. Theoretically, sites not considered for inclusion in this study could represent such extremes of frailty, where if nests are started they fail so quickly that birds are never detected and the sites are assumed unoccupied. If this is suspected, then care must be taken to limit inference to those sites that had non-zero probability of inclusion in the study.

An important assumption of this model is that causes of nest failure are correctly classified. This is unlikely to be met strictly for the majority of studies, although estimates will still be unbiased if

**Table 2.** Comparison of parameter estimates and fit statistics of three multinomial nest fate models used to analyse known-fate and known-age Piping Plover *Charadrius melodus* nest fate data ( $n = 391$ ) collected at 46 sites along the US Atlantic Coast in 2015.

Parameter	Mixed effects with covariates		Fixed effects with covariates		Intercepts only	
	Mean	sd	Mean	sd	Mean	sd
Intercepts						
Predation	-4.26	0.26	-4.16	0.18	-4.66	0.12
Abandonment	-7.38	0.81	-6.79	0.44	-5.95	0.22
Flooding	-6.77	0.65	-5.53	0.18	-5.53	0.18
Among-site variances						
Abandonment	1.13	0.70	—	—	—	—
Predation	0.60	0.21	—	—	—	—
Flooding	1.44	0.55	—	—	—	—
Fixed effects on predation						
Exclosure	-2.01	0.42*	-1.98	0.39*	—	—
0–20% vegetation	0.10	0.24	0.10	0.25	—	—
> 20% vegetation	-0.95	0.48*	-0.91	0.47*	—	—
Fixed effects on abandonment						
Exclosure	1.56	0.67*	1.32	0.50	—	—
Nest initiation date	-0.17	0.24	-0.22	0.23	—	—
Model fit statistics <sup>a</sup>						
<i>Bp</i> survival	0.61	0.49	0.95	0.23	1.00	0.01
<i>Bp</i> abandonment	0.56	0.50	0.49	0.50	0.28	0.45
<i>Bp</i> predation	0.63	0.48	0.62	0.48	0.91	0.28
<i>Bp</i> flooding	0.85	0.36	0.98	0.16	0.97	0.17
Model deviance	1263.61	14.09	1341.52	4.05	1390.66	2.48

<sup>a</sup>Bayesian *P*-value (*Bp*) estimated separately for cumulative survival, abandonment, predation and flooding probability curves. \*95% Bayesian credible interval does not overlap zero.

pairwise rates of misclassification are equivalent (Ettersson *et al.* 2007b). However, it may often be true that some fates are more likely to be misclassified, or are more likely to be mistaken for one particular alternative fate than for others. Dealing with uncertain fate has been a pervasive problem for nest survival estimation in general (Manolis *et al.* 2000, Stanley 2004) and is an especially important issue for a competing risks analysis such as this. Ettersson and Stanley (2008) described an extension of their Markov-chain model to incorporate various combinations of certain-fate nests (from videography) and other unequivocal fate evidence in their competing risks nest model. It would be possible to extend our model to incorporate rates of classification error in a manner similar to that described by Ettersson *et al.* (2007b), with misclassification rates estimated by comparing true fate determined through video with independent, field-based assessments of the same nests. However, such efforts will be beyond the scope of many studies and we thus recommend that use of our model be restricted to studies where each fate can be classified using a well-defined set of evidence criteria (i.e. fate not typically assigned by

process of elimination), and in which check intervals are short enough to reduce decay of fate evidence or occurrence of secondary fates (e.g. subsequent flooding or scavenging of an abandoned nest). Furthermore, at nests lacking strong evidence, nest fate can be left undetermined but retained in the dataset rather than making a best guess; this will inflate the variance of the estimates and lead to more conservative conclusions rather than to biased estimates resulting from misclassification.

The GOF test described in this paper is similar to that developed by Schmidt *et al.* (2010) but extended to multiple fates, and we provide the first demonstration of its ability to detect model inadequacies. In the simulation exercise, the GOF test provided strong evidence to reject the intercept-only model and moderate evidence to reject the fixed-effects-only model when used to analyse data generated using a mixed-effects model. There are no firm criteria available when using *Bp* values for assessing the fit of a model; rather, the *Bp* value is a probability statement about the difference between the realized and expected discrepancy measures (Gelman *et al.* 1996). We suggest

that repeated simulation and analysis of datasets could be used to provide custom benchmark  $Bp$  values to serve as acceptance criteria. Although we did not undertake such a full exploration,  $Bp$  values for the correct model of the simulated data ranged from 0.28 to 0.81, and for the incorrect models  $Bp$  values were  $> 0.99$  or  $< 0.07$  when both random and fixed effects were missing, and  $> 0.92$  for some fates when only random effects were missing. Thus, values  $> 0.99$  or  $< 0.01$  may be taken to suggest gross model inadequacies (as recommended by Gelman *et al.* 2004), whereas values approaching 0.05 or 0.95 may be indicative of smaller inadequacies such as overdispersion.

### Piping Plover nest fate

The GOF and model selection results indicated a strong effect of exclosure use on Piping Plover nest fate. Exclosure use resulted in increased abandonment and reduced predation rates, with a net effect of greater daily survival rates at exclosed nests. Exclosure use has been well documented to increase daily survival rates for Piping Plovers at many sites (e.g. Melvin *et al.* 1992, Barber *et al.* 2010, Doherty & Heath 2011), with recent investigations also documenting an increase in apparent abandonment attributed to exclosure use (Maslo & Lockwood 2009, Barber *et al.* 2010). Estimated site variance in the abandonment intercept parameter was 1.40, which translates to a range ( $\pm 2$  sd) of 1–6% overall probability of abandonment per nest attempt for unexclosed nests and 5–41% for exclosed nests among sites. This suggests that, although there is an overall pattern of increased abandonment with exclosure use, the severity of the problem is site-specific, and testing the fit of a random-slopes model in the future may be warranted. Possible sources of site-specific variation include exclosure dimensions and materials (Vaske *et al.* 1994, Murphy *et al.* 2003), availability of perches for raptors (Murphy *et al.* 2003) and the presence of predators that have learned to target exclosures (Niehaus *et al.* 2004).

Estimates of nest loss to different causes can provide more detailed management guidelines than examining survival alone and can reveal opposing risks associated with a single covariate, as is the case with exclosure use at Piping Plover nests. Management recommendations should be based on demographic consequences (Calvert & Taylor 2011, Cohen *et al.* 2016); thus, with adult mortality

associated with nest abandonment but not nest predation, estimating only daily nest survival probability with exclosure use could not be used to predict population-level effects of exclosure use. Rather, with this model we demonstrated that exclosures decreased predation probability but increased abandonment probability, and that abandonment probability with exclosure use varied among sites. The decision to use exclosures will rest on the site-specific trade-off between predation and abandonment risk, corresponding to the trade-off between decreasing adult survival and increasing hatching success.

This Bayesian multinomial logistic survival model provides a robust and flexible means of estimating competing probabilities of nest failure that can be generalized to other types of ragged-entry multistate or time-to-event scenarios. Multiple random effects can be incorporated to account for clustering of fate probabilities among nests within a site. Modelling covariate effects on multiple fates will generally require greater sample sizes than single-fate nest survival models or multi-fate modelling without covariates, but with adequate data this model can readily incorporate ecological and management correlates.

We thank V. Rettig, V. Turner, K. Papanastassiou, J. Bogart, K. McCall, E. Ayala, A. DeRose-Wilson, L. Johnson, C. Borck, R. Kleinart, C. Weithman, J. Parente, J. Denoncour, K. Iaquinto, B. Clifford, L. Ries, K. Holcomb, L. Baldwin, L. Zitske, K. O'Brien, S. Peterson, and K. Hojnacki for contributing ideas and data to this project. We thank M. W. Miller, R. Robinson and two anonymous reviewers for their thoughtful comments on earlier versions of this manuscript.

### REFERENCES

- Barber, C., Nowak, A., Tulk, K. & Thomas, L. 2010. Predator exclosures enhance reproductive success but increase adult mortality of Piping Plovers (*Charadrius melodus*). *Avian Conserv. Ecol.* **5**: 6.
- van der Burg, M.P. & Tyre, A.J. 2011. Integrating info-gap decision theory with robust population management: a case study using the Mountain Plover. *Ecol. Appl.* **21**: 303–312.
- Cairns, W.E. 1982. Biology and behavior of breeding Piping Plover. *Wilson Bull.* **94**: 531–545.
- Calvert, A.M. & Taylor, P.D. 2011. Measuring conservation trade-off: demographic models provide critical context to empirical studies. *Avian Conserv. Ecol.* **6**: 2.
- Cao, J. & He, C.Z. 2005. Bias adjustment in Bayesian estimation of bird nest age-specific survival rates. *Biometrics* **61**: 877–878.
- Cohen, J.B., Houghton, L.M. & Fraser, J.D. 2009. Nesting density and reproductive success of Piping Plovers in

- response to storm- and human-created habitat changes. *Wildl. Monogr.* **173**: 1–24.
- Cohen, J.B., Hecht, A., Robinson, K.F., Osnas, E.E., Tyre, A.J., Davis, C., Kocek, A., Maslo, B. & Melvin, S.M. 2016. To exclude nests or not: structured decision making for the conservation of a threatened species. *Ecosphere* **7**: e01499.
- Converse, S.J., Royle, J.A., Adler, P.H., Urbanek, R.P. & Barzen, J.A. 2013. A hierarchical nest survival model integrating incomplete temporally varying covariates. *Ecol. Evol.* **3**: 4439–4447.
- Cooch, E. & White, G. 2017. Program MARK: A Gentle Introduction. Available at: <http://www.phidot.org/software/mark/docs/book/> (accessed 29 May 2017).
- Dinsmore, S.J., White, G.C. & Knopf, F.L. 2002. Advanced techniques for modeling avian nest survival. *Ecology* **83**: 3476–3488.
- Doherty, P.J. & Heath, J.A. 2011. Factors affecting Piping Plover hatching success on Long Island, New York. *J. Wildl. Manage.* **75**: 109–115.
- Etterson, M.E. 2013. *User's Guide for MCEstimate*. US Environmental Protection Agency. Available at: [https://www.epa.gov/sites/production/files/2015-10/documents/mceestimate\\_user\\_guide.pdf](https://www.epa.gov/sites/production/files/2015-10/documents/mceestimate_user_guide.pdf) (accessed 20 July 2017).
- Etterson, M.A. & Bennett, R.S. 2005. Including transition probabilities in nest survival estimation: a Mayfield Markov chain. *Ecology* **86**: 1414–1421.
- Etterson, M.A. & Stanley, T.R. 2008. Incorporating classification uncertainty in competing-risks net-failure analysis. *Auk* **125**: 687–699.
- Etterson, M.A., Olsen, B. & Greenberg, R. 2007a. The analysis of covariates in multi-fate Markov chain nest-failure models. *Stud. Avian Biol.* **34**: 55–64.
- Etterson, M.A., Nagy, L.R. & Robinson, T.R. 2007b. Partitioning risk among different causes of nest failure. *Auk* **124**: 432–443.
- Gelman, A., Meng, X.-L. & Stern, H. 1996. Posterior predictive assessment of model fitness via realized discrepancies (with discussion). *Stat. Sin.* **6**: 733–807.
- Gelman, A., Carlin, J.B., Stern, H.S. & Rubin, D.B. 2004. *Bayesian Data Analysis*, 2nd edn. Boca Raton: Chapman & Hall/CRC.
- Guerena, K.B., Castelli, P.M., Nichols, T.C. & Williams, C.K. 2016. Factors influencing nest survival in resident Canada Geese. *J. Wildl. Manage.* **80**: 1022–1030.
- Heisey, D.M. & Fuller, T.K. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. *J. Wildl. Manage.* **49**: 668–674.
- Heisey, D.M., Shaffer, T.L. & White, G.C. 2007. The ABCs of nest survival: theory and application from a biostatistical perspective. *Stud. Avian Biol.* **34**: 13–33.
- Hoekman, S.T., Mills, L.S., Howerter, D.W., Devries, J.H. & Ball, I.J. 2002. Sensitivity analysis of the life cycle of midcontinental Mallards. *J. Wildl. Manage.* **66**: 883–900.
- Hosmer, D.W., Jr, Lemeshow, S. & Sturdivant, R.X. 2013. *Applied Logistic Regression*, 3rd edn. Hoboken: Wiley.
- Kellner, K. 2015. *jagsUI: A wrapper around 'rjags' to streamline 'JAGS' analyses*. R package version 1.3.7. Available at: <http://CRAN.R-project.org/package=jagsUI> (accessed 30 November 2015).
- Kéry, M. & Schaub, M. 2012. *Bayesian Population Analysis Using WinBUGS: A Hierarchical Perspective*. Oxford: Academic Press.
- Kuo, L. & Mallick, B. 1998. Variable selection for regression models. *Sankhyā Ser. B* **60**: 65–81.
- Liebezeit, J.R., Smith, P.A., Lanctot, R.B., Schekkerman, H., Tulp, I., Kendall, S.J., Tracy, D.M., Rodrigues, R.J., Meltotte, H., Robinson, J.A., Gratto-Trevor, C., McCaffery, B.J., Morse, J. & Zack, S.W. 2007. Assessing the development of shorebird eggs using the flotation method: species-specific and generalized regression models. *Condor* **109**: 32–47.
- Link, W.A. & Barker, R.J. 2006. Model weights and the foundations of multimodel inference. *Ecology* **87**: 2626–2635.
- Link, W.A., Cam, E., Nichols, J.D. & Cooch, E.G. 2002. Of BUGS and birds: Markov chain Monte Carlo for hierarchical modeling in wildlife research. *J. Wildl. Manage.* **66**: 277–291.
- Lloyd, P., Martin, T.E., Redmond, R.L., Langner, U. & Hart, M.M. 2005. Linking demographic effects of habitat fragmentation across landscapes to continental source-sink dynamics. *Ecol. Appl.* **15**: 1504–1514.
- Lunn, D.J., Thomas, A., Best, N. & Spiegelhalter, D. 2000. WinBUGS – A Bayesian modelling framework: concepts, structure, and extensibility. *Stat. Comput.* **10**: 325–337.
- Manolis, J.C., Andersen, D.E. & Cuthbert, F.J. 2000. Uncertain nest fates in songbird studies and variation in Mayfield estimation. *Auk* **117**: 615–626.
- Martin, T.E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecol. Monogr.* **65**: 101–127.
- Maslo, B. & Lockwood, J.L. 2009. Evidence-based decisions on the use of predator exclosures in shorebird conservation. *Biol. Conserv.* **142**: 3213–3218.
- Melvin, S.M., MacIvor, L.H. & Griffin, C.R. 1992. Predator exclosures: a technique to reduce predation at Piping Plover nests. *Wildl. Soc. Bull.* **20**: 143–148.
- Murphy, R.K., Michaud, I.M.G., Prescott, D.R.C., Ivan, J.S., Anderson, B.J. & French-Pombier, M.L. 2003. Predation on adult Piping Plovers at predator exclosure cages. *Waterbirds* **26**: 150–155.
- Natarajan, R. & McCulloch, C.E. 1999. Modeling heterogeneity in nest survival data. *Biometrics* **55**: 553–559.
- Niehaus, A.C., Ruthrauff, D.R. & McCaffery, B.J. 2004. Response of predators to Western Sandpiper nest exclosures. *Waterbirds* **27**: 79–82.
- Plummer, M. 2013. *JAGS: Just another Gibbs sampler*. Version 3.4.0. Available at: <https://sourceforge.net/projects/mcmc-jags/> (accessed 20 July 2017).
- R Core Team 2016. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available at: <https://www.R-project.org/> (accessed 30 August 2016).
- Ricklefs, R.E. 1969. *An Analysis of Nesting Mortality in Birds*. Washington, DC: Smithsonian Institution Press.
- Roche, E.A., Arnold, T.W. & Cuthbert, F.J. 2010. Apparent nest abandonment as evidence of breeding-season mortality in Great Lakes Piping Plovers (*Charadrius melodus*). *Auk* **127**: 402–410.
- Rotella, J.J., Dinsmore, S.J. & Shaffer, T.L. 2004. Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. *Anim. Biodivers. Conserv.* **27**: 187–205.



- Russell, R.E., Saab, V.A., Rotella, J.J. & Dudley, J.G. 2009. Detection probabilities of woodpecker nests in mixed conifer forests in Oregon. *Wilson J. Ornithol.* **121**: 82–88.
- Schmidt, J.H., Walker, J.A., Lindberg, M.S., Johnson, D.S. & Stephens, S.E. 2010. A general Bayesian hierarchical model for estimating survival of nests and young. *Auk* **127**: 379–386.
- Shaffer, T.L. 2004. A unified approach to analyzing nest success. *Auk* **121**: 526–540.
- Shaffer, T.L. & Thompson, F.R.I.I.I. 2007. Making meaningful estimates of nest survival with model-based methods. *Stud. Avian Biol.* **34**: 84–95.
- Smith, P.A., Bart, J., Lanctot, R.B., McCaffery, B.J. & Brown, S. 2009. Probability of detection of nests and implications for survey design. *Condor* **111**: 141–1423.
- Smith, D.H.W., Converse, S.J., Gibson, K.W., Moehrensclager, A., Link, W.A., Olsen, G.H. & Maguire, K. 2011. Decision analysis for conservation breeding: maximizing production for reintroduction of Whooping Cranes. *J. Wildl. Manage.* **75**: 501–508.
- Stanley, T.R. 2004. When should Mayfield model data be discarded? *Wilson Bull.* **116**: 267–269.
- Stephens, S.E., Rotella, J.J., Lindberg, M.S., Taper, M.L. & Ringelman, J.K. 2005. Duck nest survival in the Missouri Coteau of North Dakota: landscape effects at multiple spatial scales. *Ecol. Appl.* **15**: 2137–2149.
- Sturdivant, R.X., Rotella, J.J. & Russell, R.E. 2007. A smoothed residual based goodness-of-fit statistic for nest-survival models. *Stud. Avian Biol.* **34**: 45–54.
- Twedt, D.J., Somershoe, S.G., Hazler, K.R. & Cooper, R.J. 2010. Landscape and vegetation effects on avian reproduction on bottomland forest restorations. *J. Wildl. Manage.* **74**: 423–436.
- Vaske, J.J., Rimmer, D.W. & Deblinger, R.D. 1994. The impact of different predator exclosures on Piping Plover nest abandonment. *J. Field Ornithol.* **65**: 201–209.
- Wilson, H.M., Flint, P.L., Powell, A.N., Grand, J.B. & Moran, C.L. 2012. Population ecology of breeding Pacific Common Eiders on the Yukon-Kuskokwin Delta, Alaska. *Wildl. Monogr.* **182**: 1–28.

Received 7 February 2017;  
revision accepted 8 July 2017.  
Associate Editor: Rob Robinson.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** R code for simulating multi-fate nest data with fixed-effects covariates.

**Appendix S2.** BUGS code of multinomial nest survival model, used to analyse data simulated in Appendix S1.

**Appendix S3.** R code for analysis of real dataset with Bayesian indicator variable model selection.

**Appendix S4.** R code for goodness-of-fit tests used for the real dataset.

**Figure S1.** Interval probability of abandonment or hatch as a function of nest initiation date for Piping Plover *Charadrius melodus* nests at 46 sites along the US Atlantic Coast in 2015.

**Figure S2.** Probability of nest predation as a function of vegetation cover for Piping Plovers *Charadrius melodus* at 46 sites along the US Atlantic Coast in 2015.