

# Parameter estimation details

1	<b>1 Model</b>	<b>2</b>
2	1.1 Joint model for seed vital rates . . . . .	4
3	1.2 Viability . . . . .	7
4	1.3 Seedling survival to fruiting . . . . .	7
5	1.4 Fruits per plant & seeds per fruit . . . . .	8
6	<b>2 Model statements, implementation, and fitting</b>	<b>8</b>
7	<b>3 Computing vital rates</b>	<b>10</b>
8	3.1 Belowground vital rates - seed bank paper . . . . .	10
9	3.2 Per-capita reproductive success . . . . .	12

# 1 Model

We use observational and experimental data from 20 populations of *Clarkia xantiana* to estimate transition probabilities across the life cycle. We fit multilevel models to obtain population-specific estimates for belowground vital rates, and year- and population-specific estimates for aboveground vital rates. Because we were interested in describing the life histories of individual populations, we built separate models for each population. Our general approach applies a common model structure to partially pool observations from each population.

We first explicitly describe our formulation in terms linear mixed models before defining the joint posterior (Evans et al. 2010, Ogle and Barber 2020). We assume that the latent mean of observations in year  $j$  at a population  $k$ ,  $\theta_{jk}$ , is drawn from a normal distribution with mean  $\theta_{0,k}$  and variance  $\sigma_j^2$ .

$$\theta_{jk} = \theta_{0,k} + \epsilon_{(jk)}. \quad (1)$$

Our model includes a population-level intercept  $\theta_{0,k}$  and random effects  $\epsilon_{(jk)}$ . The random effects can be written as  $\epsilon_{(jk)} \sim N(0, \varsigma^2)$ . For the moment, we focus on describing the hierarchical structure of the model but note that we use link functions for transformation to parameters that are appropriate for the likelihoods we use to model different sets of observations (e.g. binomial for seed bag experiments; Poisson for counts of seed per fruit). We note that such a linear mixed effects model with random intercepts for years is one method commonly used to model interannual variation in demographic rates (e.g. Metcalf et al. 2015). Using hierarchical centering, the same model is rewritten as

$$\theta_{jk} = \alpha_{(jk)}. \quad (2)$$

The mean  $\theta_{jk}$ , is now drawn from a normal distribution with mean  $\alpha_{(jk)}$  and variance  $\sigma_j^2$ . We place a prior on  $\alpha_{(jk)}$  such that  $\alpha_{(jk)} \sim N(\theta_{0,k}, \varsigma^2)$ . The expressions are related by  $\alpha_{(jk)} = \theta_{0,k} + \epsilon_{(jk)}$ . We thus draw year-level means from the population-level means.

For a single population (ie. suppressing subscript  $k$ ), we write the the posterior proportional to the joint distribution as

$$[\theta_j, \theta_0, \sigma_j^2, \varsigma^2 | y_{ij}] \propto [y_{ij} | \theta_j, \sigma_j^2][\theta_j | \theta_0, \varsigma^2][\theta_0][\sigma_j^2][\varsigma^2]. \quad (3)$$

The distribution of the observations  $y_{ij}$  is conditional on the year-specific parameters  $\theta_j$  and  $\sigma_j^2$ . In turn, the year-specific parameter  $\theta_j$  is conditional on the population-specific parameters  $\theta_0$  and  $\varsigma^2$ . We placed priors on all parameters found only on the right hand side of conditional statements  $(\theta_0, \sigma_j^2, \varsigma^2)$ . In practice, we implemented this model by specifying the population- and year-levels of the model with normal distributions; for example,  $[\theta_j | \theta_0, \varsigma^2]$  is  $\theta_j \sim N(\theta_0, \varsigma^2)$ . The model thus describes a structure in which years are nested within populations.

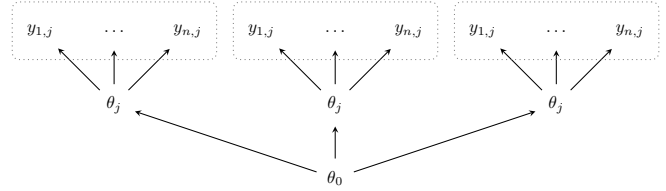


Figure 1: Graph depicting the general structure for the hierarchical models, for one population. Observations from each year,  $y_{ij}$ , are shown grouped and outlined by dotted lines. The observations are drawn from year-level parameters,  $\theta_j$ , which in turn are drawn from a population-level parameter,  $\theta_0$ . The graph omits variance terms.

## 1.1 Joint model for seed vital rates

We estimated the probabilities that seeds germinate, remain intact in the soil seed bank, and survive from seed production to the first October. We constructed models for (1) age-specific germination, (2) persistence of intact seeds, and (3) emergence of seedlings in permanent plots. We then linked these models to jointly estimate seed-related vital rates (Figure 2). The posterior and proportional joint distribution for the full model and choices for priors are specified in the Appendix: Posteriors and Appendix: Posteriors, respectively.

Seeds leave the seed bank through mortality or germination, and remain intact in the seed bank by remaining intact not germinating. In the seed bag burial experiment, we counted intact seeds for up to three years, and counted seedlings after winter rains once per year (Figure ??A). We linked the data by describing survival as the product of a continuous persistence and discrete (absence of) germination survival function (Figure ??A). We thus used the product integral of a continuous and a discrete survival function corresponding to seed survival and not germinating.

We model age-specific germination with a binomial likelihood and logit-link for the latent probability of germination. The latent probability of germination at each age is described by two hierarchical levels: the first level is the experimental years and the second (upper) level is the population. The discrete component of the survival function is the complement of the age-specific germination probability.

We model the continuous component of the survival function of intact seeds using a deterministic function. We use a Weibull survival function (Klein and Moeschberger, Smits 2015) to model the probability of seed survival after  $t$  months. The Weibull survival function is controlled by a shape and scale parameter which determine the shape and rate of the survival trajectory. The Weibull has a shape and scale parameter; we estimate a shape parameter for each population ( $\alpha_j$ ) Smits 2015. This is equivalent to assuming the rate of

change in survivorship is a population-level property but that the scale varies from year to year within each population ( $\eta_{ijk}$ ). The scale parameter is described by two hierarchical levels: the first level is the experimental year and the second (upper) level is the population.

We then combined the continuous component of the survival function, and used the complement of age-specific germination probabilities to obtain the discrete survival function describing seeds remaining in the seed bank. We model the persistence of intact seeds with a binomial likelihood and logit-link for the latent probability. The latent probability of germination at each observation instance is described by the product of the continuous and discrete components of the survival function.

We modeled seed survival like this for a few reasons. First, it allowed us to use all of the data from the seed bag experiments at once. Second, it reduced the number of parameters to estimate. Third, it allowed us to reconcile variation in observations and process: seed counts could increase from one observation period to the next and the model could decide what amount of this was due to sampling variation and what was due to the survival process.

The seed bag burial experiment allowed us to estimate seed fates starting in October after seed production but does not provide direct information about seeds between seed production and the start of the experiment. To estimate the survival of seeds from seed production to October, we augmented the model described so far with one additional component. Briefly, we used estimates for the number of seeds produced in year  $t$ , seedlings emerging in year  $t + 1$ , and our model for seed survival and germination to infer seed survival from seed production to October. We assumed that the majority of seedlings in a plot emerge from seeds produced the previous year and thus do not model germination from older seeds.

We use the counts of fruits per plant conducted in the permanent plots to get a total number of fruits per plot. We then multiply this count by the average number of seeds per fruit to get an estimate of the number of seeds produced per plot. We do this for aboveground

data in 2007 and 2008. We link this data to the number of seedlings observed in the same plots in the following year (2008 and 2009, respectively). We thus take the total number of seeds produced in year  $t$  as the number of trials in a binomial experiment for which the outcome is the number of seedlings observed in year  $t + 1$ . The probability is the product of survival from reproduction to October ( $s_0$ , estimated here), survival from October to January, and germination. We have estimates of the latter two probabilities thanks to the seed bag experiments. We link the three components and estimate the remaining term  $s_0$ .

We are unable to assess the contribution of seeds from outside the plot to the total number of seeds available. Because the number of seedlings sometimes exceed the total number of seeds, we summed across transects to get counts for the number of seeds and observed seedlings.

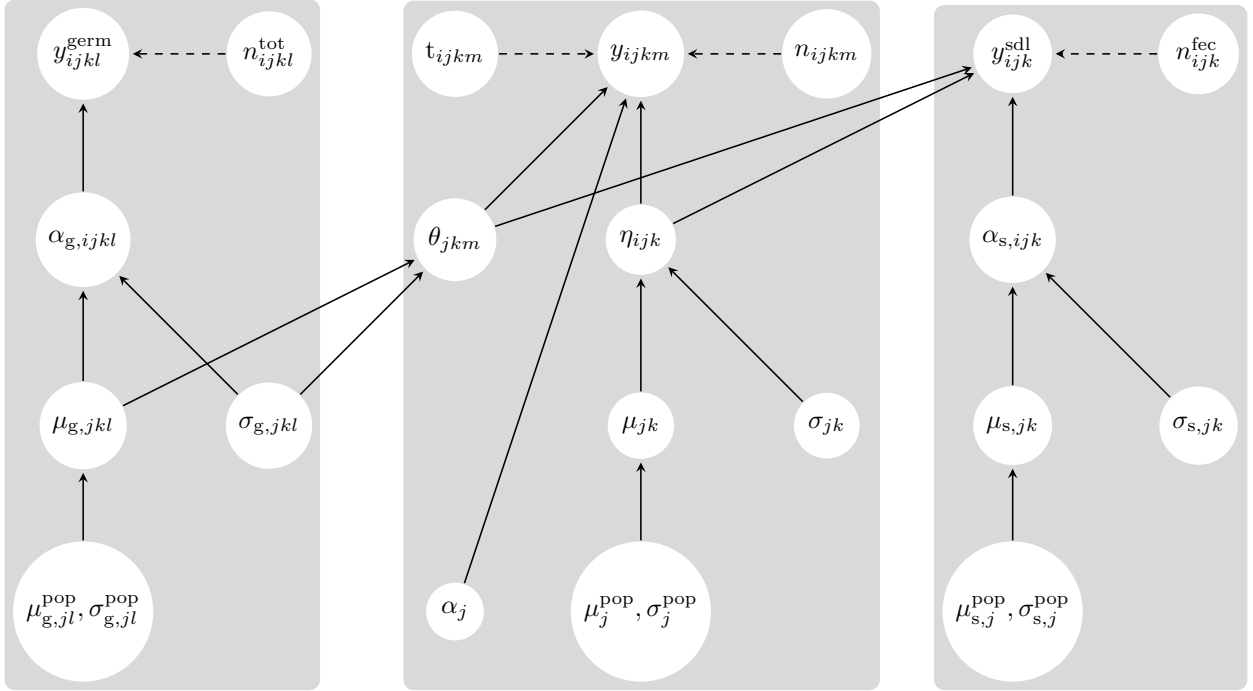


Figure 2: Directed acyclic graphs for the full model. Models for each set of data are encapsulated in a gray box; links among the datasets are shown by arrows that cross over between boxes. Solid arrows depict the relationships among random variables, and dashed arrows depict the deterministic relationships.

## 1.2 Viability

Seeds can also leave the soil seed bank through loss of viability. We estimated viability in a two-stage experiment each October after seed bags were unearthed for a second time (Figure 2C).

All data from viability trials is in the form of binomial trials: we have counts of seeds at the start and end of an experimental window of time. All models have the same structure for seeds in bag  $i$  in population  $j$  in experimental year  $k$ . If the number of seeds starting the trial (trials) is  $n_{ijk}$  and the number of seeds at the end of the trial (successes) is  $y_{ijk}$ , we write a model that has a population-level mean and year-level means drawn from the population-level distribution. Broadly, this is two-level hierarchical model with a population-level mean, and year-level means drawn from the population-level distribution. The probability of success for each bag is drawn from this year- and population-level distribution. The model uses a binomial likelihood.

## 1.3 Seedling survival to fruiting

Seedlings can perish from a multitude of causes including end-of-season drought (Geber and Eckhart 2005), intra- and interspecific competition (e.g. Geber and Eckhart 2005, James et al. 2020) small mammal herbivory (Benning et al. 2019), and fungal rust mortality (Geber and Eckhart 2005). To describe variation in survival, we wrote a model that has a population-level mean and year-level means drawn from the population-level distribution. Seedling survival to fruiting (probability of success) for each plot is drawn from this year- and population-level distribution. The model has a binomial likelihood, and thus has a similar structure as the model for

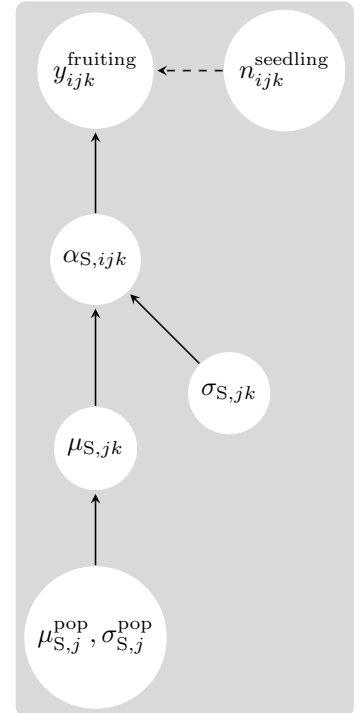


Figure 3: Directed acyclic graphs for the model for seedling survival to fruiting.

data on seed survival.

We obtain the population- and population-by-year posterior distributions of seedling survival to fruiting ( $\sigma$ ) by marginalization. We transform these posteriors to  $[0, 1]$  by taking the inverse logit; this transforms the parameters into the probability of success.

## 1.4 Fruits per plant & seeds per fruit

Seed production is the product of flowering, (self-)pollination, fruit production, and successful seed set. To describe variation in seed production, we constructed models with population-level mean and year-level means drawn from the population-level distribution. We independently modeled 3 fruit counts (total fruit equivalents, 2006-2012; undamaged fruits, 2013-present; damaged fruits, 2013-present) and 2 seed counts (seeds per undamaged fruit, 2006-present, seeds per damaged fruit, 2013-present). We used a Poisson likelihood with a log-link. We modeled sampling uncertainty with a lognormal, which draws the true number of fruits (the  $z$ s) from a distribution with the median ( $\mu$ ). Each combination of year and population is assigned its own sampling variance ( $\sigma^2$ ). Fruit and seed counts were overdispersed (show in supplement?), which the hierarchical structure of the model accommodates with each observation having a unique mean  $\lambda$  drawn from a population- and year-specific distribution (Hobbs and Hooten 2015, p. 253).

## 2 Model statements, implementation, and fitting

We include the expression for the posterior proportional to the joint distribution, and corresponding directed acyclic graphs, in Appendix: Joint Posterior. Priors for all parameters are defined in Table Priors. We applied the following principles for specifying priors: (1) we used weakly informative priors that avoided placing probability mass on biologically implausible



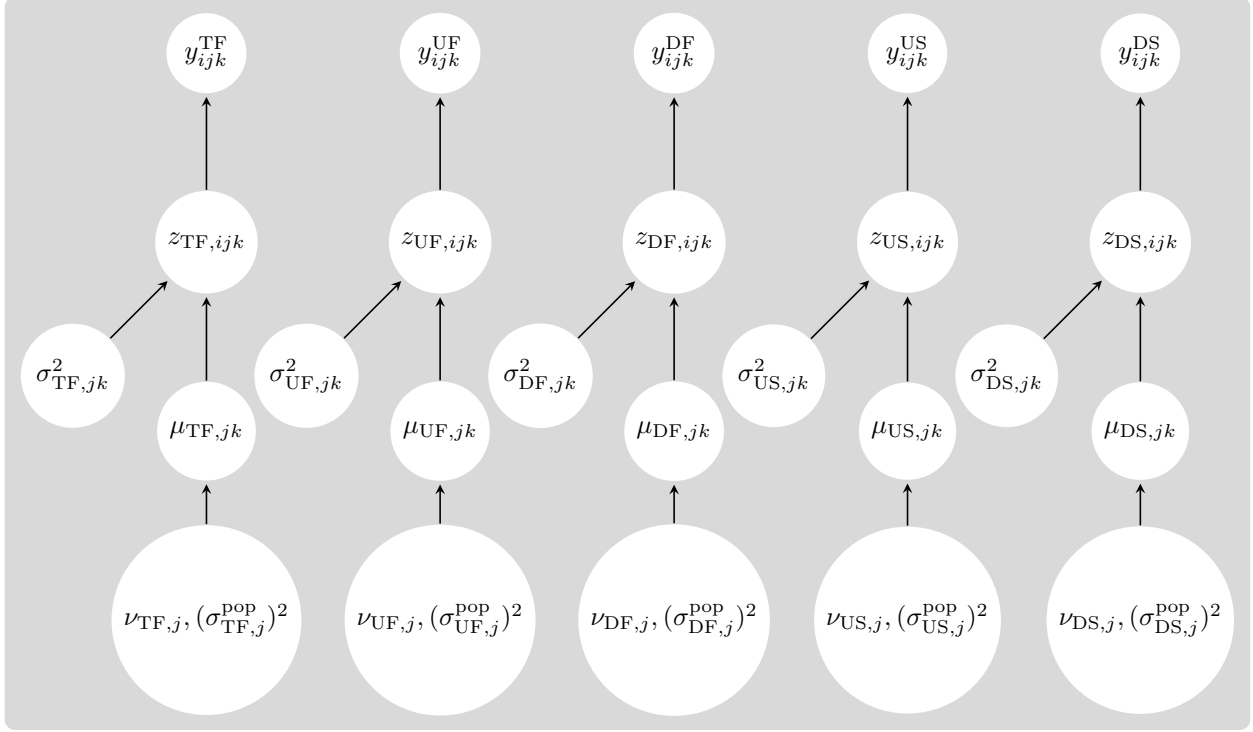


Figure 4: Directed acyclic graphs for the models for fecundity.

values (Gelman; Lemoine; Wesner and Pomeranz), (2) we placed positive, unbounded priors on variance components (REF), (3) we conducted prior predictive checks to assess the scale of priors after parameter transformation (Hobbs and Hooten; Gabry; Wesner and Pomeranz), and (4) we simulated prior predictive distributions to confirm that the joint likelihood generated data within the observed range (Gabry; Conn; Hobbs and Hooten). We provide additional detail regarding our choice of priors in Appendix: Priors.

We prepared data for analysis using the tidyverse and tidybayes packages (CITE) in R (VERSION; CITE). We wrote, fit all models, and estimated posterior distributions using JAGS (VERSION with rjags (Plummer 2016)). We randomly generated initial conditions for all parameters with a prior by drawing from the corresponding probability distribution in R before passing the initial values to rjags. We ran three chains for XX,000 iterations. The first XX,000 samples were discarded as burn-in and we sampled the following XX,000 iterations.

162 We did not thin the chains (Elder and Miller 2016).

163 We assessed convergence of the MCMC samples with visual inspection of trace plots, by  
164 calculating the Brooks-Gelman-Rubin diagnostic (R-hat), and by calculating the Heidelberg-  
165 Welch diagnostic (Elder and Miller 2016). The Gelman-Rubin diagnostic is used to assess  
166 convergence between chains and the Heidelberg-Welch for stationarity within chains. Trace  
167 plots for all chains, histograms of R-hat, and the percentage of chains that passed the HW  
168 test are shown in the appendix.

169 To evaluate our model’s fit to the data, we performed model checks that are described in  
170 full in Appendix: Model Checking. We used our posterior distribution to simulate replicate  
171 datasets based on the parameters of our model. We compared samples from the simulated  
172 datasets to the real, observed datasets using both graphical, visual checks and by calculating  
173 Bayesian  $p$ -values for test statistics calculated for the observed and simulated data. In the  
174 following section, we describe how we used the models we fit to obtain the parameters that  
175 describe the *Clarkia* life history. While we do not perform model checks for these derived  
176 quantities (e.g. winter seed survival accounting for the combined effect of seed decay and  
177 loss of viability) because we combine the output of multiple models, the model checks are  
178 still essential to determine whether our inferences are reasonable.

## 3 Computing vital rates

### 3.1 Belowground vital rates - seed bank paper

179 We used the age-specific germination probabilities, survival function, and viability estimates  
180 to account for viability in estimates for the probability of germination and survival. We first  
181 discretized the survival function to times at which we observed germination and counted  
182 seeds (January and October). Estimates of survival over these intervals are the probability

that a seed remains intact, but does not account for loss of viability. Next, we used viability estimates from October to calculate viability for January by interpolation (Figure ??D). We tested the viability of seeds in October, and were thus able to estimate the proportion of viable seeds (Figure ??B; filled points). We inferred the viability of intact seeds in January by assuming that seeds lost viability at a constant rate (exponential decay). Further, we interpolated between estimates by assuming that viability changed at a constant rate between years, and that all seeds were viable at the start of the experiment (Figure ??B; open points).

We combined the discretized survival function and viability estimates to construct a survival function for the probability that a seed remains intact and viable (Table 1, column X). Specifically, we multiplied the posteriors of the discretized survival and viability estimates. Because we combined estimates, some portions of the posterior for seed survival probability was than 1, especially for later seed ages. We restricted the posterior to be less than 1 by truncating the distribution and resampling to redistribute the probability mass. We take this step to retain parameter uncertainty about survival probability in cases where combining the estimates implies a high probability of survival. The survival function for viable seeds ( $\phi$ ) is composed of estimates of persistence over time ( $\theta$ ), estimates of viability ( $\nu$ ), and estimates of germination conditional on persistence ( $\gamma$ ).

We used the discretized survival function and age-specific germination probability to obtain the estimates of germination and seed survival required to test predictions from betting theory. Table ?? defines the age-specific germination probabilities and survival probabilities for the structured model in Eckhart et al. 2011 in terms of the survival function and age-specific germination probabilities. Figure ??E-F illustrate the relationship among the various probabilities of germination and seed survival. Estimates from the seed bag experiment correspond to the probability of germination or survival conditional on persistence (e.g.  $\gamma_1$ ). Multiplying these estimates by the probability of persistence up to a certain time gives the unconditional probability (e.g.  $\theta_1 \times \gamma_1$ ). Finally, the probability conditional

on persistence and viability is estimated by incorporating loss of viability into the survival function (e.g.  $\gamma_1/\phi_1$ ), and defines the parameters in the structured population model.

TABLE 1: Seed persistence and viability in the soil seed bank

	Persistence	Persistence & viability
Time ( $x_i$ )	$S(x_i)$	$S(x_i)$
Oct <sub>0</sub>	$\theta_0$	$\phi_0 = \theta_0$
Jan <sub>1,total</sub>	$\theta_1$	$\phi_1 = \theta_1(\gamma_1 + (1 - \gamma_1)\nu_1^{1/3})$
Jan <sub>1,intact</sub>	$\theta_2$	$\phi_2 = \theta_2\nu_1^{1/3}$
Oct <sub>1</sub>	$\theta_3$	$\phi_3 = \theta_3\nu_1$
Jan <sub>2,total</sub>	$\theta_4$	$\phi_4 = \theta_4(\gamma_2 + (1 - \gamma_2)\nu_1(\nu_2/\nu_1)^{1/3})$
Description	Parameter	Probability
July-October	$s_0$	
October-January	$s_1$	$\phi_1$
1-year old germination	$g_1$	$\gamma_1/\phi_1$
January-October	$s_2$	$\phi_3/\phi_2$
October-January	$s_3$	$\phi_4/\phi_3$

### 3.2 Per-capita reproductive success

In order to make our analysis comparable to previous empirical studies of bet hedging, we calculated per-capita reproductive success as the product of the probability of seedling survival to fruiting, fruits per plant, and seeds per fruit. We thus calculate per-capita reproductive success as the number of seeds produced per seedling, on average (e.g. Venable 2007, Gremer et al. 2014).

We used a consistent method to estimate seedling survival to fruiting throughout the experiment, and use the population- and year-level means ( $\mu_{S,jk}$ ) in our calculation. Because we estimated fruit production in 2 different ways during the study, we chose to use total fruit equivalents (TFE) per plant as our common estimate of fruit production. From 2006–2012, we used  $\mu_{TFE,jk}$  as estimated in the statistical model. From 2013–2018, we used the ratio of seeds per damaged to undamaged fruit to calculate a proportion of damaged fruits to add

223 to undamaged fruit counts, as in

$$\text{TFE} = \text{undamaged fruits} + \frac{\text{seeds per damaged fruit}}{\text{seeds per undamaged fruit}} \times \text{damaged fruits.} \quad (4)$$

224 We used posterior distributions for population- and year-level parameters (e.g.  $\mu_{\text{US},jk}$ )  
 225 for these calculations and obtained estimates of  $\mu_{\text{TFE},jk}$  for 2013–2018. Finally, we used  
 226 estimates of seeds per undamaged fruit ( $\mu_{\text{US},jk}$ ) as our estimate of seeds per fruit.

227 In terms of parameters from our statistical models, per-capita reproductive success  $F_{jk}$   
 228 at population  $j$  in year  $k$  is calculated as

$$F_{jk} = \phi_{jk} \times \lambda_{\text{TFE},jk} \times \lambda_{\text{US},jk}, \quad (5)$$

229 where

$$\begin{aligned} \phi_{jk} &= \text{logit}^{-1}(\mu_{\text{S},jk}) \\ \lambda_{\text{TFE},jk} &= \exp(\mu_{\text{TFE},jk}) \\ \lambda_{\text{US},jk} &= \exp(\mu_{\text{US},jk}). \end{aligned} \quad (6)$$

230 Our multilevel models for aboveground vital rates pooled data more strongly in years  
 231 with relatively little data. A benefit of this approach is that it implicitly corrects for varia-  
 232 tion in sample size (e.g. an observation of 0/37 seeds surviving is given more weight than an  
 233 observation of 0/1 seeds surviving). While this is beneficial for distinguishing between spuri-  
 234 ous estimates and true temporal variation in reproductive success, it may also underestimate  
 235 variation in reproductive success. At the extreme, estimates in years without any data are

236 pooled to the population-level means. Years with zero seedling survivorship would thus have  
237 estimates for fruits per plant that are pooled towards the population-mean (because there  
238 were no fruiting plants on which to count fruits).