Parameter estimation details

1 Clarkia life history

Clarkia xantiana is a winter annual that germinates with late fall and winter rains. In our study region, the Kern Valley in the southern Sierra Nevada Mountains, historically happens between October and late February or early March. Seedlings grow throughout the winter and spring, and surviving plants flower in late spring and early summer, April into early July. Pollinated fruits set seed in the early summer, June to July. Seeds of C. xantiana are produced in early summer, with fruits that dry out and gradually split open. Most seeds appear to be shed from fruits within 3-4 months after production, but can remain on the plant for up to a year. Seeds are small (< 1 mm in width) and have no structures to aid in aerial dispersal.

We represent the Clarkia xantiana as a life cycle graph (Figure 1A) that describes transitions from October of year t to October of year $t+1$ in terms of underlying vital rates. The census period occurs when the entire population is seeds, and corresponds to the time at which seed bags are placed into the field (see below). Seeds are grouped into three stages: age 0 seeds, which were produced in the current year; age 1 seeds, which were produced in the previous year; age 2+ seeds, which were produced two or more years ago. Persistence of seeds in the seed bank is represented by transitions from younger to older seeds. Production of new
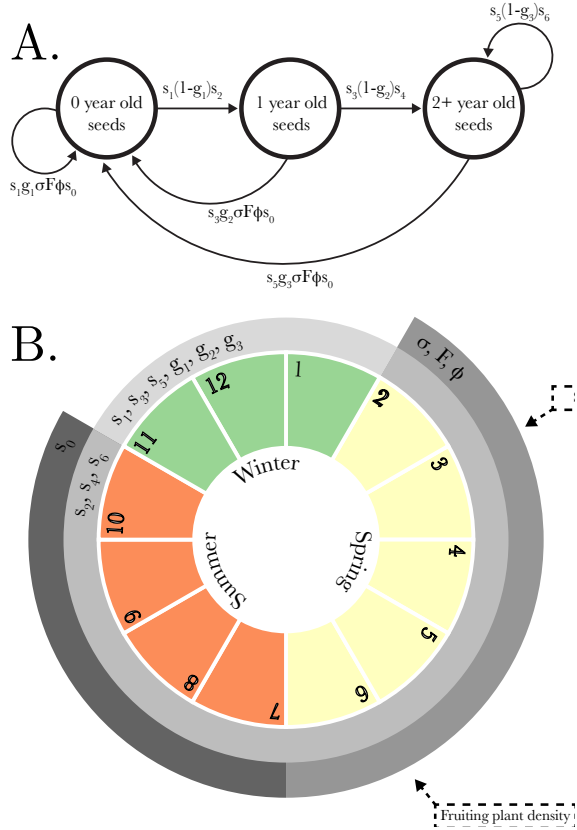

Figure 1: Diagram representations of Clarkia life cycle.

40 seeds is captured by transition to the age 0

41 seed state.

42 Transitions in the life cycle graph are the product of age-specific seed survival and

43 germination, and aboveground seedling survival to fruiting, fruit production, and seeds per

44 fruit. Seed-related rates are represented separately for age 0, 1, and 2+ seeds. Germination

45 for each age class is given as g_1, g_2, and g_3, respectively. Seed survival from seed production

46 to the first October is given as s_0, and survival from October to February is given as s_1, s_3,

47 and s_5 for age 0, 1, and 2+ seeds, respectively. Survival from February to October is given

48 as s_2, s_4, and s_6 for age 0, 1, and 2+ seeds, respectively. We assume that vital rates remain

49 unchanged after age 2. We also we assume that all plants experience the same vital rates

50 upon germination seed age at germination does not affect seedling survival to fruiting (σ),

51 fruits per plant (F), or seeds per fruit (ϕ).

The life cycle graph (Figure 1A) corresponds to the annual projection matrix

$$\boldsymbol{A} = \begin{bmatrix} s_1 g_1 \sigma F \phi s_0 & s_3 g_2 \sigma F \phi s_0 & s_5 g_3 \sigma F \phi s_0 \\ s_1(1 - g_1)s_2 & 0 & 0 \\ 0 & s_3(1 - g_2)s_4 & s_5(1 - g_3)s_6 \end{bmatrix} \tag{1}$$

52 that summarizes transitions between stages.

53 Eckhart et al. 2004 conducted a transplant experiment in two years in which seed set

54 varied ten-fold. There are additional studies that did elimination experiments (with other

55 species of Clarkia) and suggested limited role/role for seed bank because plants did or did

56 not come up with following year.

57 Lewis 1962 suggested that catastrophic selection played a major role in the dynamics

58 of *Clarkia* populations. In 13 years of data on 20 populations across the species range,

59 we observed high seedling mortality and/or low germination in at least one year in all but

four populations. Although most populations had at least some flowering plants in most years, there were also four populations in which no flowering plants were observed in the entire population. None of these populations, however, went extinct during the period of the study. Seeds can remain viable in the field and laboratory for at least 5 years, contrary to previous suggestions that seeds are unlikely to persist past a few years (Lewis 1962).
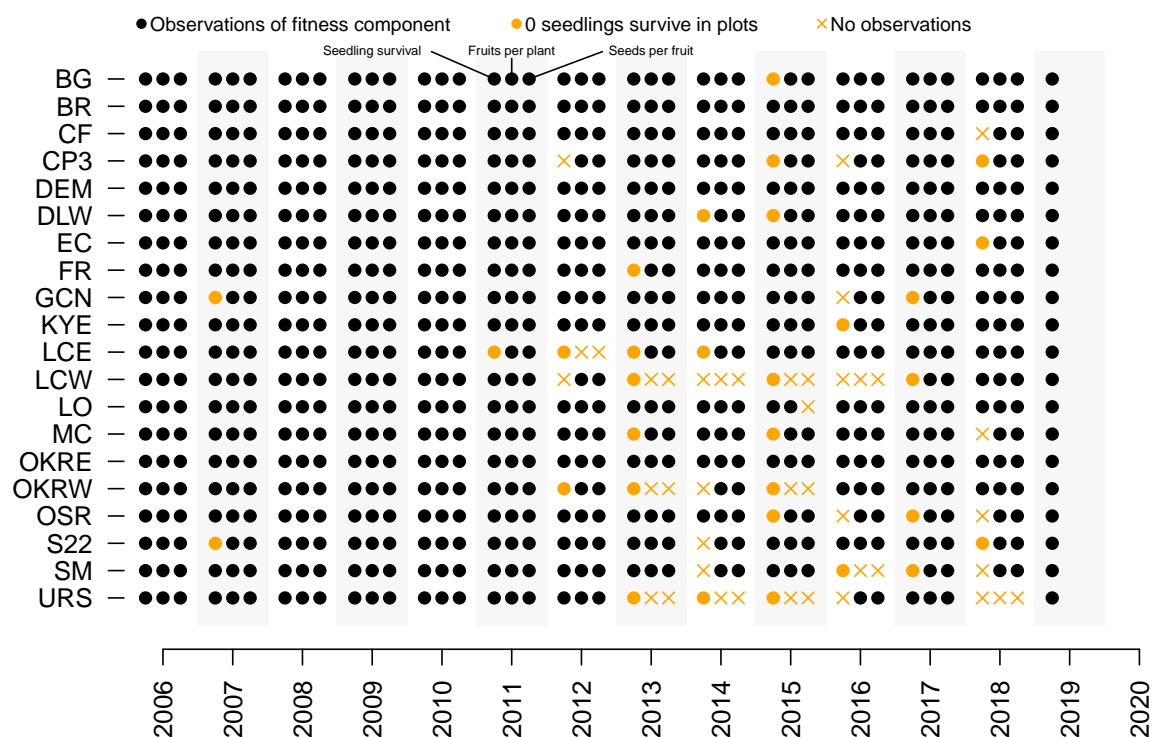

Figure 2: Summary of the aboveground observations, low fitness, and no observations.

2 Creating the dataset

We used field experiments and surveys to assemble observations of below- and above-ground demography for 20 populations of *Clarkia xantiana* (Table 1). Specifically, we used experiments to estimate transitions in the seed bank and surveys to estimate components of per-capita reproductive success. These demographic data have previously been used to test hypotheses about the geography of demography (Eckhart et al. 2011) and species distributions (Pironon et al. 2018). Here, we sought to obtain population-level estimates of germination and seed survival, and yearly estimates of per-capita reproductive success.

To estimate transitions in the seed bank, we used observations from a seed bag burial experiment conducted in all populations from 2006-2009 (Figure ??). The experiment has been previously described in Eckhart et al. 2011 and we reanalyze the data here. Geber and collaborators buried seeds in bags and unearthed 1, 2, or 3 years after being buried to count seedlings and intact, viable seeds. The experiment was repeated in 3 consecutive years and ended in 2009. We thus have 3 sets of observations associated with 1 year old seeds, 2 sets of observations associated with 2 year old seeds, and 1 set of observations associated with 3 year old seeds. We use data from the experiment to estimate age-specific germination and seed survival (see Joint model for seed vital rates) but note that we test predictions of bet-hedging theory that are based on an unstructured seed bank and use only the relevant subset of transitions in our analysis (see Computing vital rates).

To estimate per-capita reproductive success, we combine censuses of seedlings and fruiting plants, surveys of fruits per plant, and lab counts of seeds per fruit. To assess the survival of seedlings to fruiting plants, we counted seedlings and fruiting plants in 30 0.5 m^2 permanent plots from 2006–2018 (Eckhart et al. 2011). To assess seed production by plants that survive to reproduction, we counted fruits per plant on individual plants in permanent plots, and on additional haphazardly chosen plants throughout the population. We then attempted

to obtain 20-30 fruits per population, which we used to count seeds per fruit (Eckhart2011).

TABLE 1: Summary of data sets used to estimate parameters.

Parameter data	Description	Data set	Time span
SEED VITAL RATES	—	—	—
Seed survival and germination	Seed bag burial	$\mathbf{Y}_1$	2006-2009
Seed viability	Viability trials	$\mathbf{Y}_2$	2006-2009
Seed survival and germination	Seed pots	$\mathbf{Y}_3$	2013-2019
SEEDLING SURVIVAL	—	—	—
Seedling survival to fruiting	Field surveys	$\mathbf{Y}_4$	2006-2019
FRUITS PER PLANT	—	—	—
Total fruit equivalents per plant	Field surveys	$\mathbf{Y}_5$	2006-2012
Undamaged and damaged fruits per plant	Field surveys	$\mathbf{Y}_6$	2013-2019
Total fruit equivalents per plant	Extra plots	$\mathbf{Y}_7$	2006-2012
Undamaged and damaged fruits per plant	Extra plots	$\mathbf{Y}_8$	2013-2019
SEEDS PER FRUIT	—	—	—
Seeds per undamaged fruit	Lab counts	$\mathbf{Y}_9$	2006-2019
Seeds per damaged fruit	Lab counts	$\mathbf{Y}_{10}$	2013-2019

2.1 Seed bag burial experiment

We used a seed bag burial field experiment to estimate the probability of germination and survival for seeds of different ages (Figure 3A, gray panel). We buried bags with known numbers of seeds ($\boldsymbol{n} = 100$). Bags were unearthed two times during their first, second, or third year; bags that were dug up in a given year were only used to count intact seeds in that year and were removed at the end of the year. The experiment was repeated in 3 consecutive years (3 rounds) at the 20 study populations. In round 1 (started in October 2006), bags were dug up in year 1, 2, and 3. In round 2 (started in October 2007), bags were dug up in year 1 and 2. In round 3 (started in October 2008), bags were dug up in year 1. We obtained 3 sets of counts for age 1 seeds, 2 sets of counts for age 2 seeds, and 1 set of counts for age 3 seeds.

During each experimental round, we counted the number of intact seeds (y_{ijkm}) for up to 3 years. We counted the number of seeds in bag i, in population j, and in year k at

¹⁰⁴ times indexed by m, corresponding to the times at which bags were unearthed. These counts

¹⁰⁵ represent the number of seeds that remain intact in the soil seed bank. We also counted the

¹⁰⁶ number of seedlings $(y_{g,ijk})$ when we unearthed the seed bags in January. We illustrate the

¹⁰⁷ relationship between the experimental design and data in (Figure 3B), in which we show

¹⁰⁸ the hypothetical, average seed counts in seed bags from the first experimental round at one

¹⁰⁹ population. Seeds are lost from bags through physical destruction (continuous decline in

¹¹⁰ seed counts along solid lines) and germination (discrete decline in seed counts along dotted

¹¹¹ lines).

¹¹² We conducted viability experiments in each year we conducted seed burial experiments.

¹¹³ At the end of each experimental year, bags were brought to the lab and intact seeds were

¹¹⁴ tested in a two-stage viability trial (Figure 3C). In the lab, we conducted germination trials

¹¹⁵ and viability assays on subsets of the seeds from each bag to estimate the viability of the

¹¹⁶ intact seeds. First, we placed up to 15 seeds from each bag on to moist filter paper in

¹¹⁷ a disposable cup and observed the number of germinants over 10 days; we counted and

¹¹⁸ removed germinants every 2 days. For each bag, we summed the number of seeds tested and

¹¹⁹ germinating to obtain the number of trials $(n_{ijk}^{\text{test}_g})$ and successes (y_{ijk}^{germ}) summarizing the

¹²⁰ germination trials.

¹²¹ After 10 days, all remaining ungerminated seeds (up to a total of 10 seeds) were sliced in

¹²² half and individually placed into the wells of 96-well plates filled with a solution of tetrazolium

¹²³ chloride, which stains viable tissue red. [Eckhart et al. 2011: not all ungerminated seeds

¹²⁴ were tested; most were] We covered the plates with foil. Each 96-well plate contained seed

¹²⁵ from at least one bag per population of a given seed-age class. Two or three tests of up to

¹²⁶ 15 seeds each were conducted for each bag. We checked and counted for viable seeds every

¹²⁷ 2 days for 10 days. For each bag, we summed the number of seeds tested and stained to

¹²⁸ obtain the number of trials $(n_{ijk}^{\text{test}_v})$ and successes (y_{ijk}^{viab}) summarizing the viability trials.
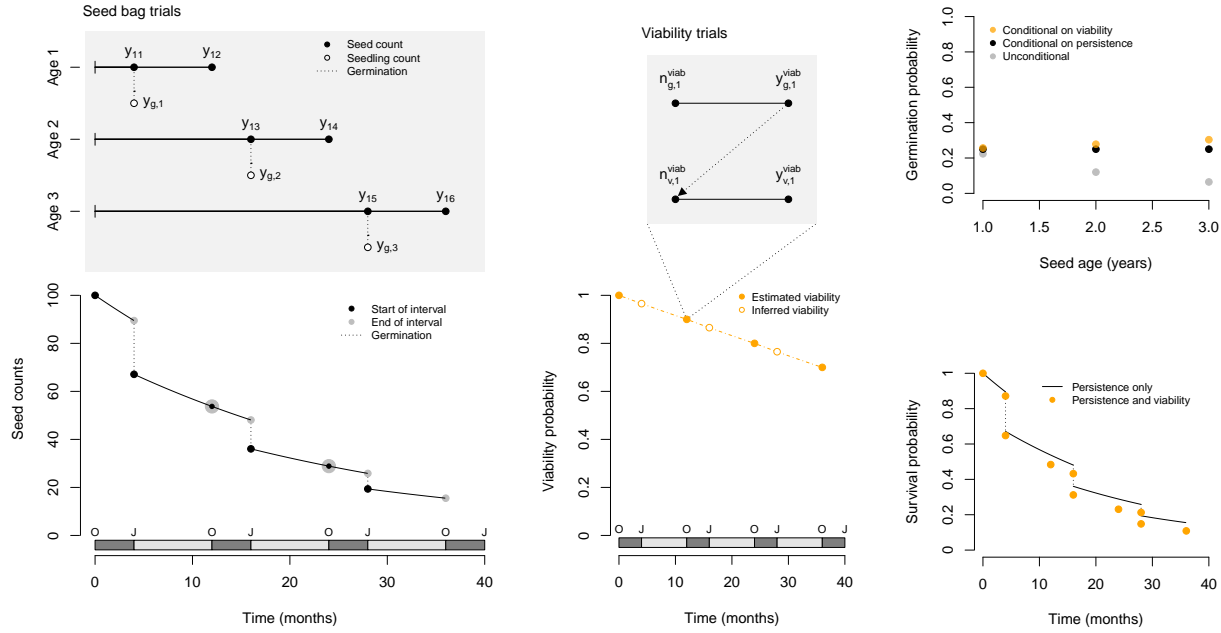
Figure 3: Summary of the seed bag burial experiments and viability trials. Figure will be labeled as (A-B: seed bag trials, C-D: viability trials, E-F: germination probability and survival probability. Add month markers to the y-axis in panels B, D, F. (A) The gray panel contains a graphical representation of the seed bag trials. Seeds were buried at the start of each experiment (100 seeds in month 0). Seed bags were unearthed and intact seeds ($y_{..}$) and germinants ($y_{g,.}$ counted. The graph below the panel shows a hypothetical survival function associated with persistence of seeds in the soil seed bank. (B) The gray panel contains a graphical representation of the viability trials. Seeds were tested in two rounds; germination trials were performed and then some or all of the ungerminated seeds were tested for viability. The graph below the panel shows hypothetical data from a series of viability trials and the interpolated, inferred viabilities at times when viability was unobserved. (C) Age-specific germination probably is summarized in three ways. (D) The graph shows the survival function for persistence of seeds in the soil seed bank (black line) and the estimated discrete survival probabilities for persistence and viability of seeds (orange points).

2.2 Seedling and fruiting plant surveys in permanent plots

129 To assess the survival of seedlings to fruiting plants, we counted seedlings and fruiting plants

130 in 30 0.5 m^2 permanent plots from 2006–2018 (Eckhart et al. 2011). Seedlings (n_{ijk}) and

131 fruiting plants (y_{ijk}) were counted in February and June, respectively, in plot i, in population

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j, and in year k. Plants in each plot are counted by a single person at each visit.

Of more than 8000 observations, there were fewer seedlings than fruiting plants in approximately 5% of observations; 50% of these had 1 fewer seedling than fruiting plant (see Supplementary Figure - could be in an appendix on the dataset). There are at least two possible mechanisms that could contribute to observations in which the number of seedlings in a plot exceeds the number of fruiting plants observed later in the same year. An observer might miss a seedling that is present, or miss a seedling because germinants remained too small to observe at the February seedling census. We assume that we did not under- or over-count fruiting plants in plots because plants stand out from the background vegetation in June. We tested the effect of (1) excluding data from plots with undercounting or (2) recoding the data such that the count of seedlings was set equal to the number of seedlings observed later in the season (see below). Future directions could include developing a model that relates our estimate of seedlings to the true number of seedlings in a plot because we sometimes observe more fruiting plants than seedlings (I had trouble developing such a model for the time being).

2.3   Surveys for fruits per plant & seeds per fruit

To assess seed production by plants that survive to reproduction, we combined estimates of fruits per plant and seeds per fruit (Eckhart2011). To determine the number of fruits per plant, we made two sets of counts at each population. First, from 2007–present, we counted the number of fruits per plant on all plants in the 0.5m^2 permanent plots. Second, from 2006–present, we counted the number of fruits per plant on additional plants that we sampled haphazardly across the site using throws of a 0.5m^2 grid. We chose to combine counts from plants in permanent and haphazardly distributed plots, because the latter often sampled a broader distribution of plant sizes and combining them allowed us to better

¹⁵⁵ estimate fruit number per plant in years with relatively few plants in permanent plots.

¹⁵⁶ From 2006–2012, we counted the number of undamaged fruits on a plant. We then took ¹⁵⁷ the damaged fruits on a plant and visually stacked them end to end to estimate how many ¹⁵⁸ additional undamaged fruits that was equivalent to (e.g. two half fruits corresponded to one ¹⁵⁹ undamaged fruit). We used this as our count (y_{ijk}^{TFE}) of total fruit equivalents on plant i, ¹⁶⁰ in population j, and in year k. From 2013–present, we counted and separately recorded the ¹⁶¹ number of undamaged (y_{ijk}^{UF}) and damaged (y_{ijk}^{DF}) fruits on a plant plant.

¹⁶² From 2006–present, we collected one undamaged fruit from each of 20-30 plants that ¹⁶³ were haphazardly chosen in each population. For each population in each year, we attempted ¹⁶⁴ to obtain 20-30 counts of seeds produced per undamaged fruit. The plants were outside ¹⁶⁵ permanent plots to avoid affecting seed input. In the lab, we counted the number of seeds ¹⁶⁶ in the fruit (y_{ijk}^{US}), corresponding to fruit i, in population j, and in year k. From 2013– ¹⁶⁷ present, we additionally collected a damaged fruit from the same plant whenever available. ¹⁶⁸ We counted the number of seeds in the fruit (y_{ijk}^{DS}), corresponding to fruit i, in population ¹⁶⁹ j, and in year k.

3   Model

¹⁷⁰ We use observational and experimental data from 20 populations of *Clarkia xantiana* to ¹⁷¹ estimate transition probabilities across the life cycle. We fit multilevel models to obtain ¹⁷² population-specific estimates for belowground vital rates, and year- and population-specific ¹⁷³ estimates for aboveground vital rates. Because we were interested in describing the life ¹⁷⁴ histories of individual populations, we built separate models for each population. Our gen- ¹⁷⁵ eral approach applies a common model structure to partially pool observations from each ¹⁷⁶ population.

¹⁷⁷ 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, θ_{jk}, is drawn from a normal distribution with mean $\theta_{0,k}$ and variance σ_j^2.

$$\theta_{jk} = \theta_{0,k} + \epsilon_{(jk)}. \tag{2}$$

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

$$\theta_{jk} = \alpha_{(jk)}. \tag{3}$$

The mean θ_{jk}, is now drawn from a normal distribution with mean $\alpha_{(jk)}$ and variance σ_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

$$[\theta_j, \theta_0, \sigma_j^2, \varsigma^2 | y_{ij}] \propto [y_{ij}|\theta_j, \sigma_j^2][\theta_j|\theta_0, \varsigma^2][\theta_0][\sigma_j^2][\varsigma^2]. \tag{4}$$

The distribution of the observations y_{ij} is conditional on the year-specific parameters θ_j and σ_j^2. In turn, the year-specific parameter θ_j is conditional on the population-specific parameters θ_0 and ς^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 distri-

Figure 4: Graph depicting the general structure for the hierarchical models, for one populatoin. Observations from each year, y_{ij}, are shown grouped and outlined by dotted lines. The observations are drawn from year-level parameters, θ_j, which in turn are drawn from a population-level parameter, θ_0. The graph omits variance terms.

butions; 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.
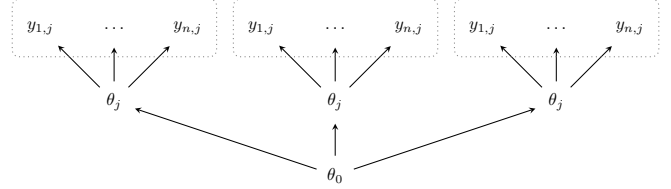
3.1   Joint model for seed vital rates

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 5). 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

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counted intact seeds for up to three years, and counted seedlings after winter rains once per year (Figure 3A). We linked the data by describing survival as the product of a continuous persistence and discrete (absence of) germination survival function (Figure 3A). 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 (α_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 (η_{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

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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
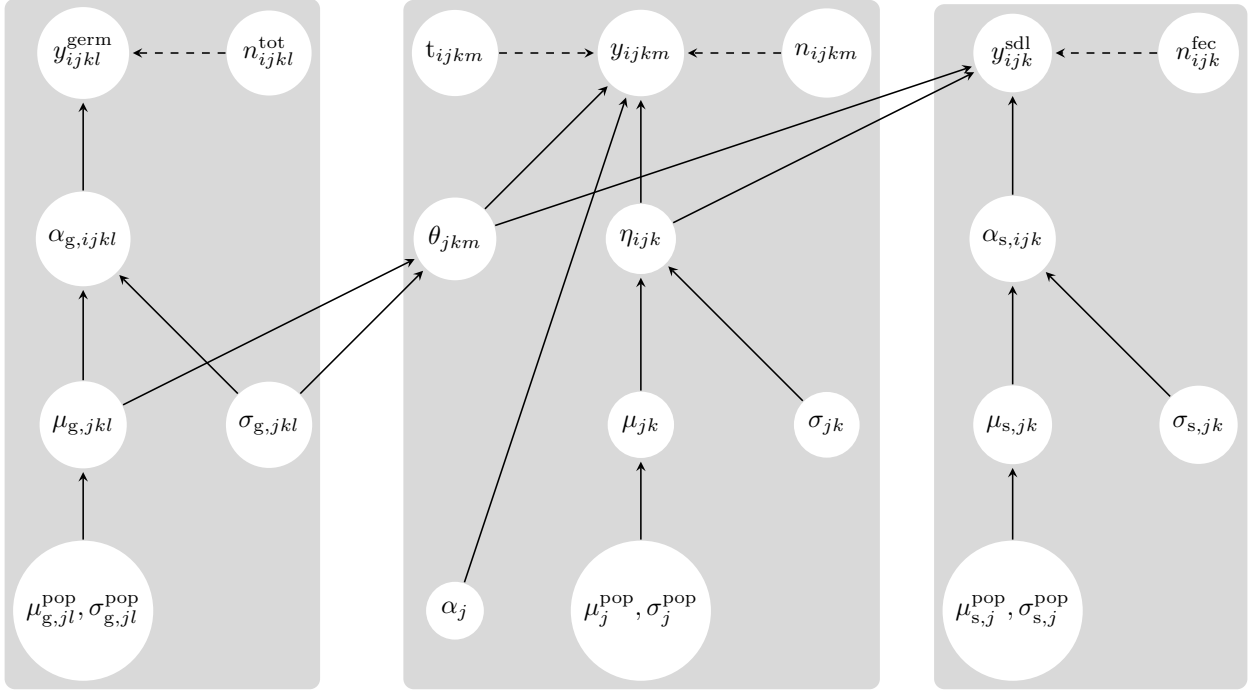
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observed seedlings.

Figure 5: 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.

3.2 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 5C).

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

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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.

3.3   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 morality (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 data on seed survival.

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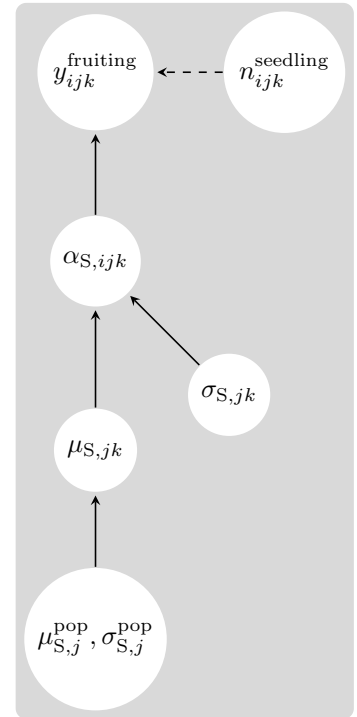

Figure 6: Directed acyclic graphs for the model for seedling survival to fruiting.

3.4   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

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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 zs) from a distribution with the median (μ). Each combination of year and population is assigned its own sampling variance (σ^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 λ drawn from a population- and year-specific distribution (Hobbs and Hooten 2015, p. 253).
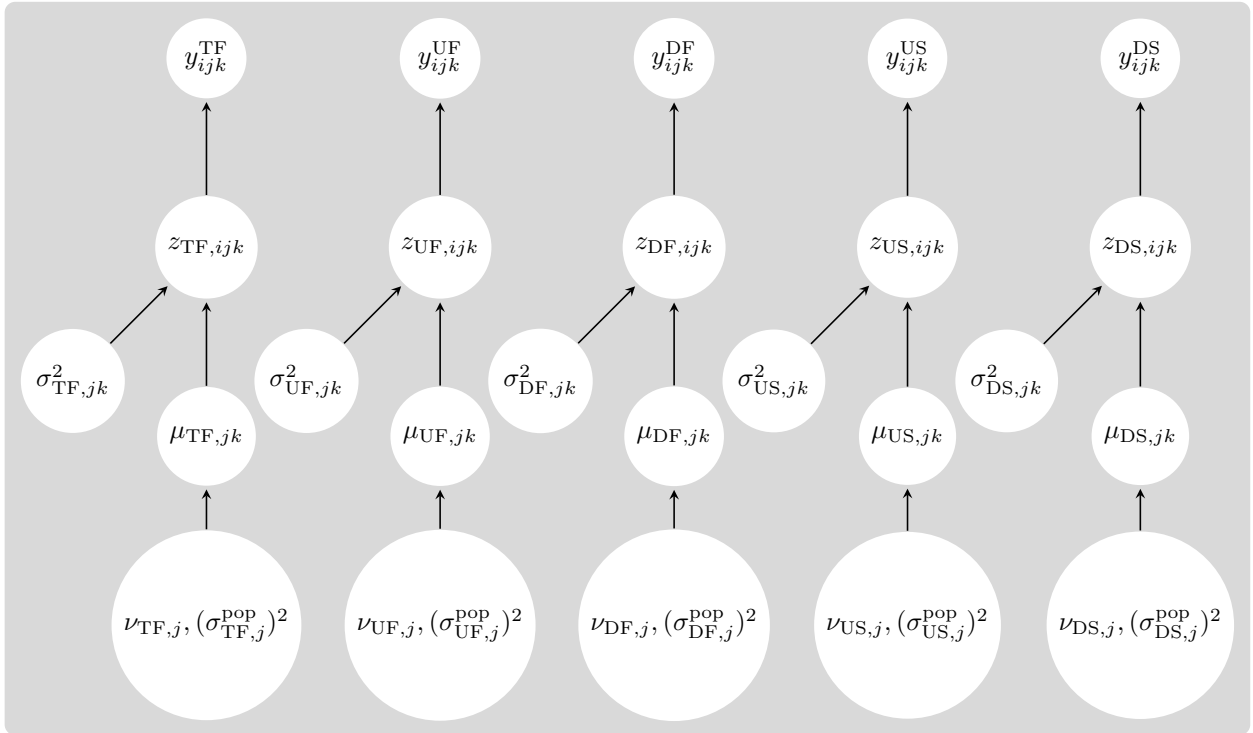

Figure 7: Directed acyclic graphs for the models for fecundity.

4 Model statements, implementation, and fitting

³⁰⁶ We include the expression for the posterior proportional to the joint distribution, and corre-

³⁰⁷ sponding directed acyclic graphs, in Appendix: Joint Posterior. Priors for all parameters are

³⁰⁸ defined in Table Priors. We applied the following principles for specifying priors: (1) we used

³⁰⁹ weakly informative priors that avoided placing probability mass on biologically implausible

³¹⁰ values (Gelman; Lemoine; Wesner and Pomeranz), (2) we placed positive, unbounded priors

³¹¹ on variance components (REF), (3) we conducted prior predictive checks to assess the scale

³¹² of priors after parameter transformation (Hobbs and Hooten; Gabry; Wesner and Pomer-

³¹³ anz), and (4) we simulated prior predictive distributions to confirm that the joint likelihood

³¹⁴ generated data within the observed range (Gabry; Conn; Hobbs and Hooten). We provide

³¹⁵ additional detail regarding our choice of priors in Appendix: Priors.

³¹⁶ We prepared data for analysis using the tidyverse and tidybayes packages (CITE) in

³¹⁷ R VERSION; CITE. We wrote, fit all models, and estimated posterior distributions using

³¹⁸ JAGS VERSION with rjags (Plummer 2016). We randomly generated initial conditions for

³¹⁹ all parameters with a prior by drawing from the corresponding probability distribution in R

³²⁰ before passing the initial values to rjags. We ran three chains for XX,000 iterations. The first

³²¹ XX,000 samples were discarded as burn-in and we sampled the following XX,000 iterations.

³²² We did not thin the chains (Elderd and Miller 2016).

³²³ We assessed convergence of the MCMC samples with visual inspection of trace plots, by

³²⁴ calculating the Brooks-Gelman-Rubin diagnostic (R-hat), and by calculating the Heidelberg-

³²⁵ Welch diagnostic (Elderd and Miller 2016. The Gelman-Rubin diagnostic is used to assess

³²⁶ convergence between chains and the Heidelberg-Welch for stationarity within chains. Trace

³²⁷ plots for all chains, histograms of R-hat, and the percentage of chains that passed the HW

³²⁸ test are shown in the appendix.

³²⁹ To evaluate our model's fit to the data, we performed model checks that are described in

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

5 Computing vital rates

5.1 Belowground vital rates - seed bank paper

We used the age-specific germination probabilities, survival function, and viability estimates to account for viability in estimates for the probability of germination and survival. We first discretized the survival function to times at which we observed germination and counted 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 3D). We tested the viability of seeds in October, and were thus able to estimate the proportion of viable seeds (Figure 3B; 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 3B; open points).

We combined the discretized survival function and viability estimates to construct a

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survival function for the probability that a seed remains intact and viable (Table 3, 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 (ϕ) 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 bet-hedging theory. Table 4 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 3E-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. γ_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. γ_1/ϕ_1), and defines the parameters in the structured population model.

TABLE 2: Seed persistence and viability in the soil seed bank

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	Persistence	Persistence & viability
Time (x_i)	$S(x_i)$	$S(x_i)$
Oct_0	θ_0	$\phi_0 = \theta_0$
$\mathrm{Jan}_{1,\text{total}}$	θ_1	$\phi_1 = \theta_1(\gamma_1 + (1-\gamma_1)\nu_1^{1/3})$
$\mathrm{Jan}_{1,\text{intact}}$	θ_2	$\phi_2 = \theta_2\nu_1^{1/3}$
Oct_1	θ_3	$\phi_3 = \theta_3\nu_1$
$\mathrm{Jan}_{2,\text{total}}$	θ_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	ϕ_1
1-year old germination	g_1	γ_1/ϕ_1
January-October	s_2	ϕ_3/ϕ_2
October-January	s_3	ϕ_4/ϕ_3

5.2 Belowground vital rates - all

We used the age-specific germination probabilities, survival function, and viability estimates to account for viability in estimates for the probability of germination and survival. We first discretized the survival function to times at which we observed germination and counted 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 3D). We tested the viability of seeds in October, and were thus able to estimate the proportion of viable seeds (Figure 3B; 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 3B; 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. 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,

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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 (ϕ) is composed of estimates of persistence over time ($\theta_.$), estimates of viability ($\nu_.$), and estimates of germination conditional on persistence ($\gamma_.$).

TABLE 3: Seed persistence and viability in the soil seed bank

	Persistence	Persistence & viability
Time (x_i)	$S(x_i)$	$S(x_i)$
Oct_0	θ_0	$\phi_0 = \theta_0$
$\mathrm{Jan}_{1,\mathrm{total}}$	θ_1	$\phi_1 = \theta_1(\gamma_1 + (1 - \gamma_1)\nu_1^{1/3})$
$\mathrm{Jan}_{1,\mathrm{intact}}$	θ_2	$\phi_2 = \theta_2\nu_1^{1/3}$
Oct_1	θ_3	$\phi_3 = \theta_3\nu_1$
$\mathrm{Jan}_{2,\mathrm{total}}$	θ_4	$\phi_4 = \theta_4(\gamma_2 + (1 - \gamma_2)\nu_1(\nu_2/\nu_1)^{1/3})$
$\mathrm{Jan}_{2,\mathrm{intact}}$	θ_5	$\phi_5 = \theta_5\nu_1(\nu_2/\nu_1)^{1/3}$
Oct_2	θ_6	$\phi_6 = \theta_6\nu_2$
$\mathrm{Jan}_{3,\mathrm{total}}$	θ_7	$\phi_7 = \theta_7(\gamma_3 + (1 - \gamma_3)\nu_2(\nu_3/\nu_2)^{1/3})$
$\mathrm{Jan}_{3,\mathrm{intact}}$	θ_8	$\phi_8 = \theta_8\nu_2(\nu_3/\nu_2)^{1/3}$
Oct_3	θ_9	$\phi_9 = \theta_9\nu_3$

We used the survival function and age-specific germination probabilities to obtain the parameters in the structured population model for *Clarkia xantiana* ssp. *xantiana*. Table 4 defines the age-specific germination probabilities and survival probabilities for the structured model in Eckhart et al. 2011 in terms of the survival function (Table 3) and age-specific germination probabilities.

TABLE 4: Structured model parameters conditional on persistence and viability

Parameter	Probability
g_1	γ_1/ϕ_1
g_2	γ_2/ϕ_4
g_3	γ_3/ϕ_7
s_1	ϕ_1
s_2	ϕ_3/ϕ_2
s_3	ϕ_4/ϕ_3
s_4	ϕ_6/ϕ_5
s_5	ϕ_7/ϕ_6
s_6	ϕ_9/ϕ_8

Figure 3E-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. γ_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. γ_1/ϕ_1), and defines the parameters in the structured population model.

5.3 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

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of seeds per damaged to undamaged fruit to calculate a proportion of damaged fruits to add

to undamaged fruit counts, as in

$$\text{TFE} = \text{undamaged fruits} + \frac{\text{seeds per damaged fruit}}{\text{seeds per undamaged fruit}} \times \text{damaged fruits}. \tag{5}$$

We used posterior distributions for population- and year-level parameters (e.g. $\mu_{\text{US},jk}$)

for these calculations and obtained estimates of $\mu_{\text{TFE},jk}$) for 2013–2018. Finally, we used

estimates of seeds per undamaged fruit ($\mu_{\text{US},jk}$) as our estimate of seeds per fruit.

In terms of parameters from our statistical models, per-capita reproductive success F_{jk}

at population j in year k is calculated as

$$F_{jk} = \phi_{jk} \times \lambda_{\text{TFE},jk} \times \lambda_{\text{US},jk}, \tag{6}$$

where

$$\phi_{jk} = \text{logit}^{-1}(\mu_{\text{S},jk})$$
$$\lambda_{\text{TFE},jk} = \exp(\mu_{\text{TFE},jk}) \tag{7}$$
$$\lambda_{\text{US},jk} = \exp(\mu_{\text{US},jk}).$$

Our multilevel models for aboveground vital rates pooled data more strongly in years

with relatively little data. A benefit of this approach is that it implicitly corrects for varia-

tion in sample size (e.g. an observation of 0/37 seeds surviving is given more weight than an

observation of 0/1 seeds surviving). While this is beneficial for distinguishing between spuri-

ous estimates and true temporal variation in reproductive success, it may also underestimate

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variation in reproductive success. At the extreme, estimates in years without any data are pooled to the population-level means. Years with zero seedling survivorship would thus have estimates for fruits per plant that are pooled towards the population-mean (because there were no fruiting plants on which to count fruits).