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# BAYESIAN ESTIMATION OF A DEMOGRAPHIC MATRIX MODEL FROM STAGE-FREQUENCY DATA

KEVIN GROSS,[1,4] BRUCE A. CRAIG,[2] AND WILLIAM D. HUTCHISON[3]

[1]*Departments of Zoology and Statistics, University of Wisconsin, Birge Hall, 430 Lincoln Drive, Madison, Wisconsin 53706 USA*
[2]*Department of Statistics, Purdue University, West Lafayette, Indiana 47907 USA*
[3]*Department of Entomology, University of Minnesota, St. Paul, Minnesota 55108 USA*

*Abstract.* Demographic matrix models are standard tools for analyzing the dynamics of age- or stage-structured populations. Here, we present a method for estimating the average vital rates that parameterize a demographic matrix using a series of measurements of population size and structure (an "inverse problem" of demographic analysis). We join a deterministic, density-independent demographic matrix model with a stochastic observation model to write a likelihood function for the matrix parameters given the data. Adopting a Bayesian perspective, we combine this likelihood function with prior distributions for the model parameters to produce a joint posterior distribution for the parameters. We use a numerical technique (Markov chain Monte Carlo) to estimate and analyze the posterior distribution, and from this we calculate posterior distributions for functions of the demographic matrix, such as the population multiplication rate, stable stage distribution, and matrix sensitivities. Although measurements of population size and structure rarely contain enough information to estimate all the parameters in a matrix precisely, our analysis sheds light on the information that the data do contain about the vital rates by quantifying the precision of the parameter estimates and the correlations among them. Moreover, we show that matrix functions such as the population multiplication rate and matrix sensitivities can still be estimated precisely despite sizable uncertainty in the estimates of individual parameters, permitting biologically meaningful inference. We illustrate our approach for three populations of pea aphids (*Acyrthosiphon pisum*).

*Key words:* Acyrthosiphon pisum; *Bayesian statistics; demographic matrix models; estimation; Markov chain Monte Carlo; pea aphid; population dynamics; stage-frequency data.*

## INTRODUCTION

Demographic matrix models (Leslie 1945, Caswell 2001) are widely used tools for analyzing the population dynamics of age- or stage-structured populations. Matrix models use the average vital rates of individuals in separate age classes or stages to project the population dynamics that would ensue if these vital rates remained constant. These projected dynamics can be summarized by measures such as the long-term population multiplication rate, the stable stage distribution, and sensitivities of population growth to individual vital rates, which are all functions of the demographic matrix itself (Caswell 2001). Because matrix models provide a simple yet flexible framework for linking individual vital rates to population dynamics, they have gained widespread popularity and use (e.g., Werner and Caswell 1977, Crouse et al. 1987, Doak et al. 1994, Tuljapurkar and Caswell 1997, Caswell 2001 and references therein).

Constructing a matrix model entails estimating the stage-specific vital rates of individuals, such as probabilities of growth and survival, and fecundities. Here, we consider estimating these vital rates from a series of measurements of population size and stage structure. Because we are trying to estimate individual demographic rates on the basis of population dynamics, this problem belongs to the broader class of "inverse" problems in the analysis of structured populations, so named because they are the inverse of projecting dynamics from demographic rates (Keller 1976, Wood 1997).

As a motivating example, we consider three populations of pea aphids in alfalfa. Pea aphids, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae), are common agricultural pests in south-central Wisconsin. Pea aphids pass through four juvenile nymphal instars before becoming adults, making them suitable for stage-structured models. Adults give birth to live nymphs during the summer, and there is no pupal stage. Summer reproduction is parthenogenetic (all adults can reproduce), with adults capable of larvipositing up to seven nymphs per day (Hutchison and Hogg 1984). This short generation time and high fecundity give aphids the potential for rapid population growth. Alfalfa fields in southern Wisconsin are mowed and harvested approximately every six weeks.

In the early 1980s, one of us (W. D. Hutchison) monitored aphid populations during part of one mowing

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[4] E-mail: kgross@students.wisc.edu

TABLE 1. Measurements of population size and structure for three aphid populations.

| Field and year | Day | Aphids per stem | | | Stage structure | | |
|---|---|---|---|---|---|---|---|
| | | Stems | Mean | Standard deviation | Instars I/II | Instars III/IV | Adults |
| Arlington 1980 | 1 | 192 | 0.45 | NA | 46 | 46 | 12 |
| | 6 | 192 | 2.18 | 3.32 | 296 | 60 | 52 |
| | 9 | 192 | 5.08 | 8.17 | 506 | 122 | 60 |
| | 13 | 192 | 18.75 | 27.29 | 232 | 96 | 42 |
| | 16 | 192 | 41.48 | 50.05 | 337 | 129 | 67 |
| | 20 | 192 | 66.39 | 127.69 | 324 | 138 | 48 |
| | 24 | 64 | 106.87 | 84.79 | 286 | 138 | 70 |
| Madison 1980 | 1 | 192 | 0.91 | 2.24 | 110 | 20 | 19 |
| | 4 | 192 | 2.01 | 4.38 | 258 | 67 | 48 |
| | 8 | 192 | 8.13 | 9.98 | 993 | 313 | 197 |
| | 11 | 192 | 25.39 | 31.59 | 367 | 104 | 88 |
| | 15 | 64 | 110.31 | 85.51 | 329 | 167 | 74 |
| | 19 | 64 | 201.76 | 156.08 | 348 | 198 | 81 |
| Arlington 1982 | 1 | 192 | 0.72 | 0.50 | 133 | 41 | 22 |
| | 4 | 192 | 1.03 | 1.78 | 245 | 73 | 28 |
| | 8 | 192 | 2.45 | 2.24 | 166 | 92 | 31 |
| | 11 | 192 | 3.48 | 3.76 | 233 | 138 | 62 |
| | 15 | 192 | 5.30 | 4.90 | 319 | 176 | 44 |
| | 18 | 192 | 4.30 | 3.83 | 214 | 266 | 49 |

cycle in three alfalfa fields—fields in Arlington and Madison, Wisconsin in 1980 and an Arlington field in 1982 (Table 1). In each field, aphid densities were measured every 3–5 d for 18–26 d (seven surveys total in Arlington 1980, six surveys apiece in Madison 1980 and Arlington 1982). At each survey, aphids were counted on either 64 or 192 alfalfa stems divided equally among 16 sectors of the field. Only the sample means and variances of the number of aphids per stem were retained for future analysis. Additionally, different samples of aphids were collected from each sector, returned to the laboratory, identified to instar, and pooled counts were recorded. Further details of the field study can be found in Hutchison and Hogg (1985).

Our goal is to estimate a demographic matrix for the initial density-independent growth phase of each of these three populations. By doing so, we hope to learn as much as we can about the average stage-specific vital rates that produced these dynamics. Also, we want to use the matrix to estimate the population's long-term growth rate and stable stage distribution. In addition, we would like to compare the sensitivities of the population growth rate to growth rates of young and old juveniles, information that could be useful when identifying potential biological control agents. Because we are only interested in the density-independent growth phase of the dynamics, we restrict our attention to the first five surveys for each population, ignoring the final one or two surveys that clearly suggest density dependence.

Several authors have considered the inverse problem in the context of matrix models, with reviews provided by Manly (1990: Chapter 6) and Caswell (2001: Section 6.2). Lefkovitch (1965) initially used multiple regression to estimate a stage-structured demographic matrix from a series of equally spaced measurements of population size and structure. More recently, Caswell and Twombly (1989) and Twombly (1994) have modified the regression approach to stabilize the parameter estimates and accommodate time-varying vital rates, and Ennola et al. (1998) have introduced an estimation strategy based on a Kalman filter. An extensive literature also exists on the related but distinct inverse problem of estimating mortality rates in a stage-structured population when recruitment into the population is not explicitly modeled as a function of the number of reproductive adults (Wood et al. 1989, Wood and Nisbet 1991, Wood 1994; also Manly 1989, 1990, 1997, and references therein).

A central theme arising from the study of inverse problems is that vital rates are not fully identifiable knowing only population dynamics, because multiple combinations of vital rates can produce the same dynamics (Caswell and Twombly 1989, Wood et al. 1989, Wood 1994, 1997). Wood's (1994) example is helpful—a bear population with two bears yesterday and three today may have experienced a single birth overnight, 101 births and 100 deaths, or any combination in between. While this lack of full identifiability does not render attempts to estimate a demographic matrix from population dynamics data futile, it does beg the questions of which, if any, matrix parameters can be estimated precisely, how precise these estimates will be, and if it is possible to estimate matrix functions such as population growth rate even with sizable uncertainty about some of the parameters.

Here, we present an approach to estimating a demographic matrix from measurements of population size and structure that sheds light on these questions. We combine a deterministic, density-independent demographic matrix model with a stochastic observation model to produce a probability model for the obser-

vations that depends on the matrix parameters. The likelihood function that results could be analyzed from a frequentist perspective (similar to the maximum likelihood approach described in Caswell 2001: Section 6.2.3), but here we adopt a Bayesian view, combining the likelihood with a prior distribution of the matrix parameters to produce a joint posterior distribution for the parameters (Gelman et al. 1995). Our analysis is enabled by Markov chain Monte Carlo (MCMC), a numerical technique used to estimate distributions (such as the posterior distributions here) that are too complicated to analyze analytically (Gilks et al. 1996). We illustrate this approach by fitting separate matrix models to each of our three aphid populations.

The paper is arranged as follows. First, we present the particular matrix models for the pea aphid populations, and show how these are combined with observation models to write a likelihood function for the matrix parameters given the data. We then use Bayesian inference, enabled by MCMC, to estimate the posterior distributions for the matrix parameters and several matrix functions, such as the population multiplication rate. The details of the MCMC are given in the Appendix. We also include a small simulation study to explore the behavior of our method in more depth. We conclude by discussing both the specific implications and assumptions of this modeling study, and more general issues about Bayesian estimation of demographic models.

## Model Development

### *Demographic matrix model*

The demographic matrix model describes how a population changes over time as a function of the average vital rates of individuals (Caswell 2001). These vital rates are written as the demographic matrix **A**. For all but the first row of **A**, the matrix parameter in the $i$th row and $j$th column of **A** is the probability that an individual in stage $j$ at time $t$ moves to stage $i$ at time $t + 1$. Parameters in the first row of **A** are the sums of the probabilities that individuals stay in or regress to stage 1, plus the average number of offspring produced by individuals in each stage (assuming individuals born between time $t$ and time $t + 1$ are in the first stage at time $t + 1$). Writing the population densities in each stage at time $t$ as the vector $\mathbf{n}(t)$, population dynamics can be modeled by the iterative matrix multiplication $\mathbf{n}(t + 1) = \mathbf{A}\mathbf{n}(t)$.

For the pea aphids, we use a matrix model with a daily time step. In order to reduce the number of parameters to be estimated, we combine the first and second instars into the first life stage, and the third and fourth instars into the second life stage. Adults constitute the third stage of the model. Using conventional notation (Caswell 2001), our matrix is then

$$\mathbf{A} = \begin{pmatrix} P_1 & 0 & F \\ G_1 & P_2 & 0 \\ 0 & G_2 & P_3 \end{pmatrix} \tag{1}$$

where $P_i$ is the probability that an aphid in stage $i$ at time $t$ remains in stage $i$ until time $t + 1$, $G_i$ is the probability that an aphid in stage $i$ at time $t$ grows to stage $i + 1$ by time $t + 1$, and $F$ is the mean number of surviving offspring produced daily by an adult. Because this is a deterministic model, the vector of initial densities $\mathbf{n}(1)$ and the transition matrix **A** completely specify the entire time series of population dynamics. The units of $\mathbf{n}(t)$ are aphids per stem.

If the matrix **A** does not change over time, the population will eventually grow at its asymptotic population multiplication rate, $\lambda$, which is equal to the dominant eigenvalue of **A** (Caswell 2001). The distribution of individuals among stages will converge to the stable stage distribution **w**, which equals the dominant right eigenvector of **A**. The amount by which an incremental change in a matrix parameter $a_{ij}$ changes $\lambda$ is called the sensitivity of $\lambda$ to $a_{ij}$, and can be calculated by Caswell's (1978) formula:

$$\frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\langle \mathbf{v}, \mathbf{w} \rangle} \tag{2}$$

where **v** is the dominant left eigenvector of **A**, and $\langle \cdot, \cdot \rangle$ is an inner product. As the notation suggests, these matrix sensitivities are the partial derivatives of $\lambda$ with respect to the matrix parameters.

### *Observational model*

In order to link the matrix model with the data, we need a probability model that quantifies the likelihood of the collected data given the actual size and stage-structure of the population. Each survey provides two pieces of data—the average number of aphids counted per stem and the number of aphids in each stage from the collected subsample. Because aphids are aggregated among stems (Ives et al. 2000), we use the negative binomial distribution as a phenomenological model for the distribution of aphids among stems (May 1978). Assuming that the number of aphids counted on any one stem is conditionally independent of the numbers of aphids found on other stems, for a survey $i$ at time $t_i$, the probability of observing a total of $x_i$ aphids on $n_s$ stems is

$$P_{nb}(x_i \mid \mathbf{n}(t_i), k) = \binom{kn_s + x_i - 1}{x_i} \left(\frac{k}{\mu_{t_i} + k}\right)^{kn_s} \left(\frac{\mu_{t_i}}{\mu_{t_i} + k}\right)^{x_i} \tag{3}$$

where $P_{nb}(\cdot)$ denotes the negative binomial probability mass function, $\mu_{t_i}$ is the mean number of aphids per stem (equal to the sum of the components of $\mathbf{n}(t_i)$), and $k$ is the clumping parameter that determines the degree of aggregation of aphids among stems. The variance in

the number of aphids per stem is equal to $\mu_{t_i} + \mu_{t_i}^2/k$, so the distribution of aphids becomes more aggregated as $k$ becomes smaller, and approaches a Poisson distribution as $k \to \infty$ (Johnson et al. 1992). The parameter $\mu_{t_i}$ is determined by the matrix model, and thus changes for each survey, while we assume that $k$ remains constant over time.

For the stage-classified sample, we assume that the sizes of all aphids collected are conditionally independent. We use a multinomial distribution as a probability model for the observed stage structure, with each stage's probability of occurrence equal to the relative abundance of that stage in the population vector $\mathbf{n}(t)$. That is to say, the probability of collecting $y_{i,1}$, $y_{i,2}$, and $y_{i,3}$ aphids from stages 1–3 at time $t_i$ is

$$P_{\text{mn}}(\mathbf{y}_i \,|\, n(t_i)) = \begin{pmatrix} (y_{i,1} + y_{i,2} + y_{i,3})! \\ y_{i,1}!y_{i,2}!y_{i,3}! \end{pmatrix} \left(\frac{n_1(t_i)}{n_\bullet(t_i)}\right)^{y_{i,1}} \left(\frac{n_2(t_i)}{n_\bullet(t_i)}\right)^{y_{i,2}} \left(\frac{n_3(t_i)}{n_\bullet(t_i)}\right)^{y_{i,3}} \tag{4}$$

where $P_{\text{mn}}(\cdot)$ is a multinomial probability mass function, $n_1(t_i)$, $n_2(t_i)$, and $n_3(t_i)$ are the mean number of aphids per stem in stages 1–3, respectively, at time $t_i$, and $n_\bullet(t_i)$ is their sum.

Putting the demographic and observational models together produces a probability model for the data that depends on the demographic matrix, the negative binomial aggregation parameter $k$, and the initial population vector $\mathbf{n}(1)$. Assuming conditional independence among surveys, this probability model is

$$\begin{aligned} P(x_1, \ldots, x_5, \mathbf{y}_1, \ldots, \mathbf{y}_5 \,|\, \mathbf{A}, k, \mathbf{n}(1)) &= \prod_{i=1}^{5} P_{\text{nb}}(x_i \,|\, \mathbf{n}(t_i), k) P_{\text{mn}}(\mathbf{y}_i \,|\, \mathbf{n}(t_i)) \\ &= \prod_{i=1}^{5} P_{\text{nb}}(x_i \,|\, \mathbf{A}^{t_i - 1}\mathbf{n}(1), k) P_{\text{mn}}(\mathbf{y}_i \,|\, \mathbf{A}^{t_i - 1}\mathbf{n}(1)) \end{aligned} \tag{5}$$

where the survey index $i$ runs from 1 to 5.

## Bayesian Inference

Bayesian analysis treats model parameters as random quantities and analyzes the distribution of the model parameters conditional on the data (Gelman et al. 1995, Carlin and Louis 2000). The components of a Bayesian analysis are the prior distribution of the parameters, denoted here by $\pi(\mathbf{A}, k, \mathbf{n}(1))$, the likelihood of the data, given by Eq. 5, and the posterior distribution for the parameters given the data, denoted $\pi(\mathbf{A}, k, \mathbf{n}(1) \,|\, x_1, \ldots, x_5, \mathbf{y}_1, \ldots, \mathbf{y}_5)$. These components are linked by Bayes' rule

$$\pi(\mathbf{A}, k, \mathbf{n}(1) \,|\, x_1, \ldots, x_5, \mathbf{y}_1, \ldots, \mathbf{y}_5) \propto P(x_1, \ldots, x_5, \mathbf{y}_1, \ldots, \mathbf{y}_5 \,|\, \mathbf{A}, k, \mathbf{n}(1)) \pi(\mathbf{A}, k, \mathbf{n}(1)) \tag{6}$$

(Gelman et al. 1995). The prior distribution reflects what is known about the parameters before analyzing the data, and the posterior combines this information with the information about the parameters in the data. The posterior distribution can also be used to find posterior distributions for functions of the demographic matrix, such as $\lambda$, $\mathbf{w}$, and matrix sensitivities.

Because the probability model in Eq. 5 is complicated, the posterior cannot be calculated directly. Instead, we estimate the posterior with a numerical technique called Markov chain Monte Carlo (MCMC) (Metropolis et al. 1953, Hastings 1970, Geman and Geman 1984, Gilks et al. 1996). MCMC produces a pseudo-random sample of the matrix parameters drawn from the posterior distribution. As the size of the MCMC sample increases, the sample distribution approximates the posterior distribution. The MCMC sample can also be used to estimate posterior distributions for matrix functions by calculating the matrix function for each draw in the MCMC sample. Details of our MCMC algorithm can be found in the Appendix. Below, we discuss prior construction and posterior estimation for one population, though we conducted three separate analyses, one for each population.

### *Prior distributions*

Bayesian statistics allow prior knowledge about model parameters to be introduced through so-called "informative" priors. Informative priors use previous knowledge to quantify the degree to which some parameter values are more likely than others. Here, however, we use vague or flat priors for all of the parameters except the aggregation parameter $k$. Flat priors place equal prior probability on all parameter values within a plausible range. For example, the parameters $P_1$ and $G_1$ must both be positive, and their sum must be less than, 1, because they represent transition rates from the same stage. Therefore, we used a flat prior constrained by $P_1 \geq 0$, $G_1 \geq 0$, and $P_1 + G_1 \leq 1$ (a so-called Dirichlet(1,1,1) distribution [Johnson and Kotz 1972]). We used this same prior for the $(P_2, G_2)$ pair, and a uniform prior on the interval from 0 to 1 for $P_3$. For the fecundity $F$, we used a uniform prior on the interval from 0 to 10, setting an upper bound of 10 nymphs per day as a fecundity well above the maximum fecundity of seven nymphs per day observed by Hutchison and Hogg (1984) in benign outdoor insectaries. Thus, although the prior for $F$ is flat, it is not completely uninformed by prior knowledge. Similarly, for each component of the initial density vector $\mathbf{n}(1)$, we used a uniform prior on the interval from 0 to 100, with 100 aphids per stem much greater than any plausible initial density for any stage. With the exception of the $(P_1, G_1)$ and $(P_2, G_2)$ pairs, all prior distributions were mutually independent.

For $k$, we used informative priors based on the sample variances of the number of aphids counted per stem, because these sample variances contained information about $k$ that could not be included otherwise. (The sam-

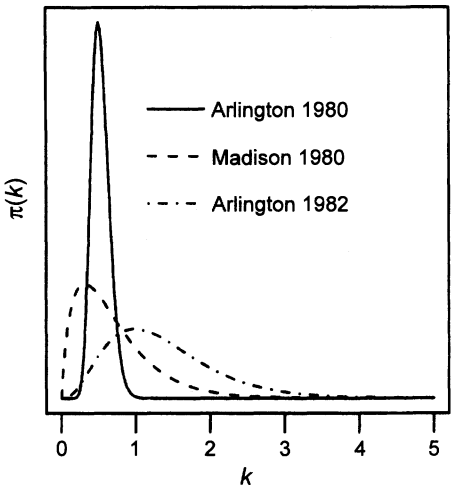


FIG. 1. Prior probability densities for the negative binomial aggregation parameter, $k$.

ple variance cannot easily be placed into the likelihood function because the sample mean and variance of a random sample are not sufficient statistics for a negative binomial distribution with both parameters unknown [Willson et al. 1986].) This approach is similar to so-called empirical Bayes methods, which use the data to specify the prior (Casella 1985). For each aphid population, we used the sample means and variances from the stem counts to calculate method-of-moments estimates of $k$ for each of the first five surveys where sample means and variances were available. We treated each estimate as a realization of a Gamma random variable, and found the maximum likelihood estimates of the parameters for the Gamma distribution given the estimates of $k$. These Gamma distributions were used as the priors for $k$ (Fig. 1). Prior means for $k$ are 0.532, 0.701, and 1.367 for Arlington 1980, Madison 1980, and Arlington 1982, respectively.

To ensure that our results were robust to our choices of noninformative priors, we fit each model a second time with an alternative, and presumably equally noninformative, prior specification. These alternative priors included a Dirichlet(½,½,½) prior on the ($P_1$, $G_1$) and ($P_2$, $G_2$) pairs, a Beta (½,½) prior on $P_3$, a uniform prior on (0, 20) for $F$, and independent uniform priors on (0, 10) for each component of $\mathbf{n}(1)$.

### *Posterior analysis*

For each population, the population multiplication rate, stable stage distribution, and sensitivities of the multiplication rate to $G_1$ and $G_2$ were calculated for each recorded chain value. Posterior means for these quantities and the matrix parameters themselves were estimated by the mean of the recorded chain values. The 95% posterior intervals for each scalar estimand were estimated by the shortest of three candidate intervals—the intervals bounded by the parameter's least possible value and the 95th percentile of the MCMC sample, the 2.5th and 97.5th percentiles of the MCMC sample, and the 5th percentile of the MCMC sample and parameter's largest possible value. (Posterior intervals are the Bayesian analog of frequentist confidence intervals; they contain 95% of the posterior probability for a parameter [Casella and Berger 1990]). Marginal posterior densities were estimated with normal-kernel smoothing (Wand 1994, Venables and Ripley 1997) and the posterior probability that $\partial\lambda/\partial G_1 \geq \partial\lambda/\partial G_2$ was estimated by tallying the fraction of recorded values for which this was the case. For comparison's sake, the prior densities of $\lambda$, $\mathbf{w}$, $\partial\lambda/\partial G_1$, and $\partial\lambda/\partial G_2$ induced by the prior on $\mathbf{A}$ were estimated by drawing 10 000 random matrices from the prior on $\mathbf{A}$ and calculating each of these quantities.

### *Model validation and tests of assumptions*

Our model makes a series of assumptions, some of which we were able to assess quantitatively. The matrix model itself assumes that a stage-structured matrix model with constant vital rates is appropriate for the initial portion of the observed dynamics. To check this assumption, we estimated posterior predictive distributions for hypothetical additional data by simulating a new data set for each recorded iteration of the MCMC sampler. (Posterior predictive distributions are marginal distributions for hypothetical additional data averaged over the posterior distribution of the parameters [Gelman et al. 1995: Section 6.3].) We calculated means and posterior intervals for the posterior predictives, and compared these with the observed data.

The probability distributions in the observational component of the model (Eqs. 3–5), though natural ones, also make assumptions about the survey data. In particular, the negative binomial and multinomial models in Eqs. 3 and 4 make specific assumptions about how the probability distributions of possible observations changed as the size and stage-structure of the aphid population changed, and Eq. 5 assumes conditional independence within and among surveys. To assess the negative binomial assumption in Eq. 3, we estimated posterior predictive distributions for the sample variances of the stem counts for each survey, and compared these with observed values. A similar comparison for the multinomial model in Eq. 4 was not possible, so instead we examined the robustness of the model to violations of the multinomial assumption by re-fitting each model with a Dirichlet-multinomial distribution for the stage-categorized sample (Gelman et al. 1995: Chapter 12). (A Dirichlet-multinomial is a multivariate extension of the Beta-Binomial that permits greater variability in the data [Johnson et al. 1997: Section 13.1].) We did not examine the consequences of violating the conditional independence assumption in Eq. 5.

### *Simulation study*

To observe the behavior of our model under a wider set of conditions, we conducted a limited simulation

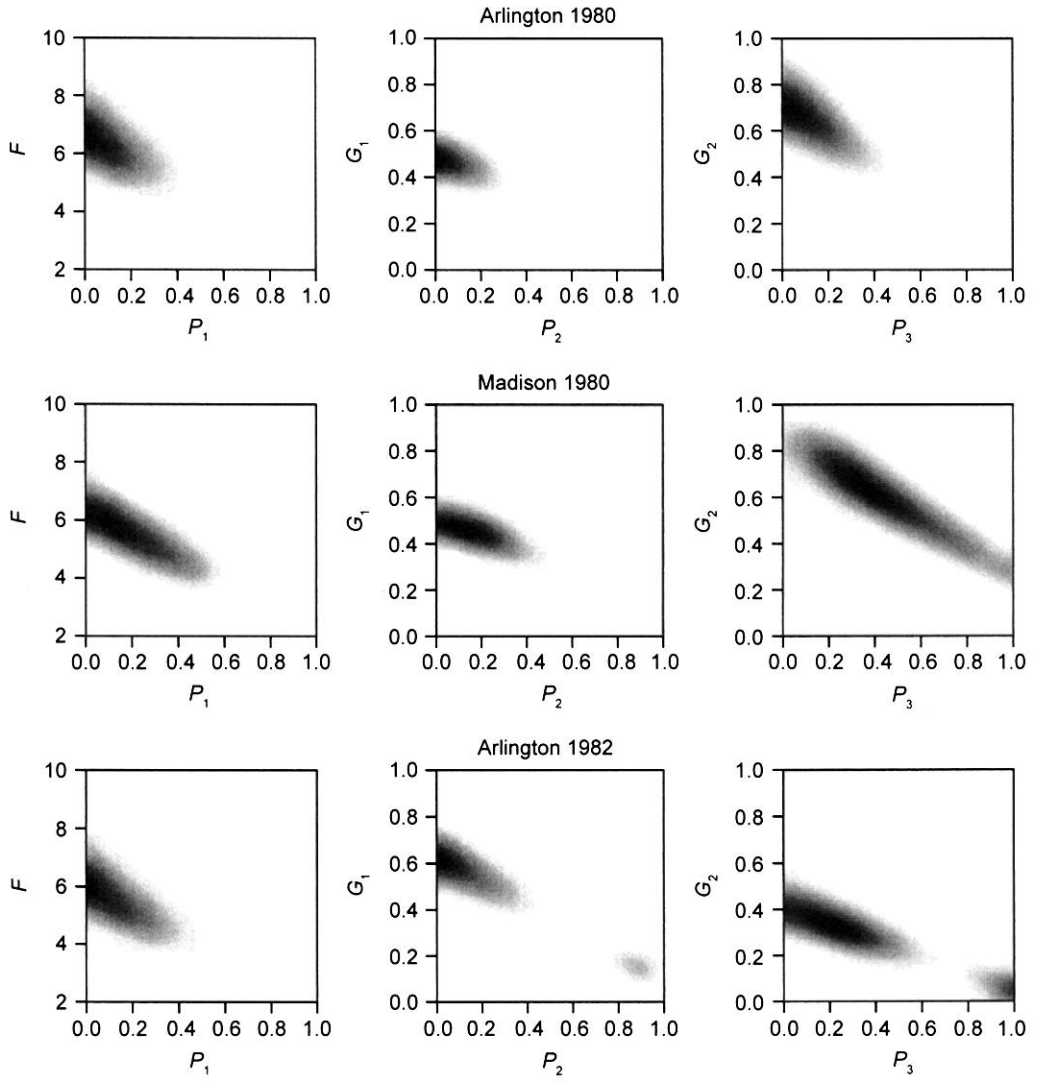


FIG. 2. Smoothed bivariate posterior density estimates for matrix parameters. Darker regions indicate greater posterior density. Each row of panels corresponds to a single population.

study. For this simulation, we selected five different demographic matrices at random from the prior of **A**, conditional upon $0.5 \leq \lambda \leq 2$. Components of the initial population vector $\mathbf{n}(1)$ were drawn from a uniform distribution on (0, 1), and values of $k$ were drawn from the prior distribution of $k$ for the Madison 1980 population (Fig. 1). For each of these five sets of parameters, we simulated five data sets with the same structure as the Madison 1980 data (i.e., the same timetable for data collection, and the same numbers of stems and size-classified aphids at each survey), for a total of 25 simulated data sets. For each simulated data set, we estimated posterior distributions for the matrix parameters using the same priors as we did for the actual data (and the Madison 1980 prior for $k$), and the same MCMC algorithm.

## RESULTS

For all three populations, the joint posterior distributions of the matrix parameters were dominated by strong negative correlations between pairs of parameters sharing the same row of **A** (Fig. 2). Across the three populations, the estimated posterior correlation coefficients averaged $-0.76$ for the $(P_1, F)$ pair, $-0.80$ for the $(G_1, P_2)$ pair, and $-0.88$ for the $(G_2, P_3)$ pair. No other pair of matrix parameters had an average posterior correlation coefficient with a magnitude greater than 0.35.

Marginal posterior densities provided moderately precise information about some of the matrix parameters. For example, the estimated posterior standard deviation of $G_1$ from the Arlington 1980 population was only 0.04, and a 95% posterior interval ranged

TABLE 2. Posterior means and marginal 95% posterior intervals (PI) for matrix parameters and functions.

| | Arlington 1980 | | Madison 1980 | | Arlington 1982 | |
|---|---|---|---|---|---|---|
| Parameter | Mean | 95% (PI) | Mean | 95% (PI) | Mean | 95% (PI) |
| $P_1$ | 0.127 | (0, 0.319) | 0.204 | (0, 0.462) | 0.174 | (0, 0.538) |
| $F$ | 6.270 | (4.916, 7.818) | 5.547 | (4.170, 6.811) | 5.371 | (2.839, 6.964) |
| $G_1$ | 0.458 | (0.370, 0.539) | 0.449 | (0.348, 0.528) | 0.522† | (0.138, 0.679)† |
| $P_2$ | 0.092 | (0, 0.234) | 0.171 | (0, 0.370) | 0.209† | (0, 0.868)† |
| $G_2$ | 0.650 | (0.465, 0.827) | 0.613 | (0.312, 0.852) | 0.307† | (0.055, 0.456)† |
| $P_3$ | 0.139 | (0, 0.335) | 0.429 | (0.085, 0.920) | 0.303† | (0, 0.956)† |
| $k$ | 0.540 | (0.331, 0.799) | 0.874 | (0, 1.890) | 0.624 | (0, 1.372) |
| $n_1(1)$ | 0.190 | (0.135, 0.254) | 0.641 | (0.516, 0.794) | 0.491 | (0.366, 0.624) |
| $n_2(1)$ | 0.185 | (0.137, 0.244) | 0.110 | (0.071, 0.161) | 0.142 | (0.098, 0.191) |
| $n_3(1)$ | 0.048 | (0.029, 0.070) | 0.098 | (0.062, 0.141) | 0.066 | (0.041, 0.105) |
| $\lambda$ | 1.345 | (1.318, 1.373) | 1.423 | (1.384, 1.458) | 1.176 | (1.147, 1.207) |
| $w_1$ | 0.641 | (0.613, 0.672) | 0.633 | (0.611, 0.656) | 0.580 | (0.549, 0.609) |
| $w_2$ | 0.234 | (0.210, 0.258) | 0.227 | (0.209, 0.246) | 0.312 | (0.285, 0.340) |
| $w_3$ | 0.125 | (0.106, 0.145) | 0.140 | (0.125, 0.155) | 0.108 | (0.090, 0.127) |
| $\partial\lambda/\partial G_1$ | 0.895 | (0.758, 1.067) | 0.838 | (0.635, 0.995) | 0.603 | (0.463, 0.802) |
| $\partial\lambda/\partial G_2$ | 0.638 | (0.503, 0.831) | 0.634 | (0.475, 0.898) | 1.079 | (0.743, 1.771) |

† Bimodal distributions.

from 0.37 to 0.54. For other parameters, though, the posterior was barely more informative than the prior (e.g., $P_3$ for Madison 1980, with a 95% posterior interval covering 0.08 to 0.92). On the whole, posteriors for the 1980 populations suggested small probabilities of juvenile survival without growth ($P_1$, $P_2$) and adult survival ($P_3$), with large probabilities of juvenile growth ($G_1$, $G_2$) and large fecundities ($F$) (Table 2).

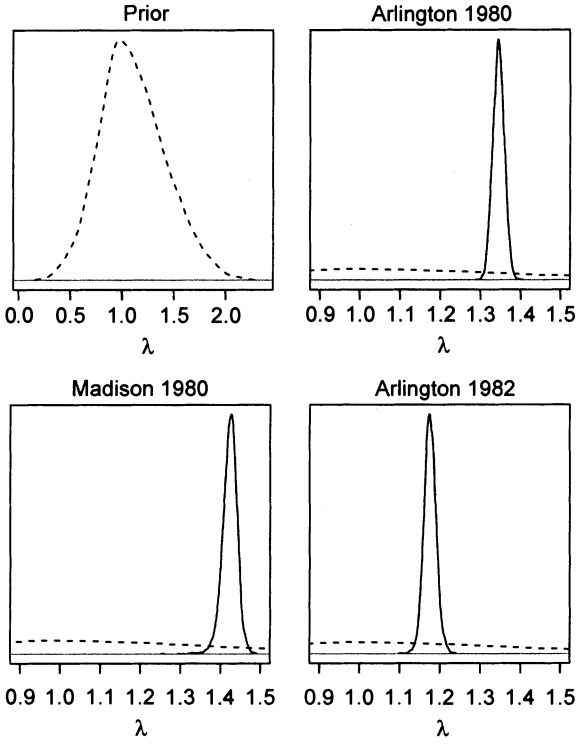


FIG. 3. Smoothed prior and posterior densities for the population multiplication rate, $\lambda$, for each of the three populations. The dashed lines in the posterior panels show the prior distribution of $\lambda$ in the plotted range.

Inference about the vital rates for the Arlington 1982 population was not as straightforward because the posterior distribution for the ($G_1$, $P_2$) and ($G_2$, $P_3$) pairs had two modes. One mode suggested moderate probabilities of juvenile survival with rapid growth, while the other mode suggested very high juvenile survival with very slow development. Using the boundary $P_2 + P_3 = 1$ to divide the two regions, there was a 90% posterior probability that the parameter values lay in the $P_2 + P_3 < 1$ region. The posterior means and 95% posterior intervals for these parameters should be interpreted with caution, because they mask the bimodal nature of the posterior distribution.

In contrast to the marginal posterior distributions of the matrix parameters, the posterior distributions for $\lambda$ (Fig. 3) and $\mathbf{w}$ (Fig. 4) were concentrated on a small set of possible values. By comparison, the induced prior distributions on $\lambda$ and $\mathbf{w}$ were disperse, suggesting that the reduced variability in the posterior is attributable to information in the data. Among the three populations, $\lambda$ was largest for Madison 1980 and smallest for Arlington 1982. For Arlington 1982, the marginal posterior of $\lambda$ appeared unimodal, despite the bimodality of the posterior for $\mathbf{A}$. All three posterior distributions for $\mathbf{w}$ suggested that young nymphs were most abundant, and adults least abundant, in the stable stage distribution. The posteriors also indicated that the Arlington 1982 stable stage distribution contained slightly more older nymphs and fewer younger nymphs than either of the 1980 populations.

Posterior distributions of the sensitivities of $\lambda$ to $G_1$ and $G_2$ differed among the three populations (Fig. 5). The estimated posterior probabilities that $\lambda$ was more sensitive to $G_1$ than to $G_2$ were 96%, 87%, and 2% for Arlington 1980, Madison 1980, and Arlington 1982

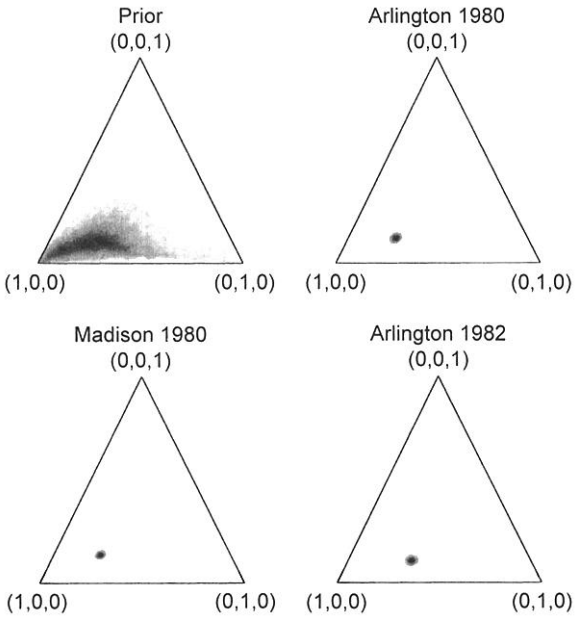


FIG. 4. Smoothed prior and posterior density estimates of the stable stage distribution, **w**. The lower left vertices of the triangles correspond to distributions composed entirely of young juveniles, the lower right vertices to populations of all old juveniles, and the upper vertices to populations of all adults. Darker regions indicate greater posterior density.

populations, respectively. For comparison, λ was more sensitive to $G_1$ in 50% of the prior samples. In both the prior and posteriors, estimates of these two sensitivities were negatively correlated.

For our purposes, the aggregation parameter $k$ and the initial density estimates in **n**(1) were nuisance parameters. Nevertheless, comparing their posterior distributions to their priors was informative. For the 1980 populations, the posteriors for $k$ resembled the priors (Fig. 6, Table 2), indicating that the mean stem counts contained little additional information about the aggregation of aphids among stems. For the Arlington 1982 population, the posterior density for $k$ was shifted toward smaller values relative to the prior distribution, suggesting even greater clumping of aphids among stems. However, this smaller estimate of $k$ may also have been caused by a lack of model fit (see *Discussion: Model assumptions, validation, and possible violations*).

Posterior predictive distributions for both aphid densities and stage-structure showed little variability, and were consistent with the observed data (Fig. 7). Additionally, 95% posterior predictive intervals for the sample variances of the stem counts covered the observed sample variance for 11 of 14 surveys, with observed sample variances falling below the lower bounds of the posterior intervals in three surveys from Arlington 1982.

Refitting the model with a Dirichlet-multinomial distribution for the stage-categorization increased the width of the marginal posterior intervals for matrix parameters by an average of 53%. However, none of the posterior means for λ changed by more than 1.2%, and the width of posterior intervals for λ increased by an average of 9%. Posterior means for each of the components of **w** changed by an average of 3%, although the width of their marginal posterior intervals increased by an average of 160%.

Re-fitting the models with our alternative prior specification did not change the structure of the posterior for **A**, although it did result in some minor changes in marginal distributions, especially for Arlington 1982. For the 1980 populations, posterior means for matrix parameters changed by an average of 1.0%, and the width of marginal posterior intervals changed by an average of 2.4%. For Arlington 1982, however, posterior means changed by an average of 7.0%, and posterior intervals shrunk by an average of 12.1%. The parameters λ and **w** were less sensitive to the change in prior specification. Across all populations, posterior means and posterior interval widths changed by an average of 0.4% and 12.3% for λ, and by an average of 0.2% and 2.1% for the components of **w**.

In our simulation study, the joint posterior distribution of the matrix parameters displayed the same structure as it did for the actual data, with strong negative correlations between matrix parameters sharing the same row. Fig. 8 shows the marginal posterior distributions for the ($G_1$, $P_2$) pair for all simulations; marginal posteriors for ($P_1$, $F$) and ($P_2$, $G_3$) behaved similarly. Regions of high posterior density covered the true parameter values in most cases, with the true value

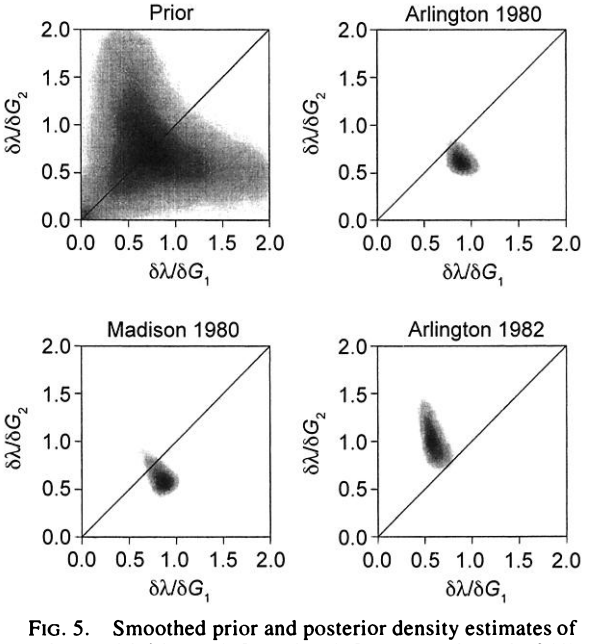


FIG. 5. Smoothed prior and posterior density estimates of matrix sensitivities $\partial\lambda/\partial G_1$ and $\partial\lambda/\partial G_2$. Approximately 24% of the prior density lies outside the region shown. Darker regions indicate greater posterior density.

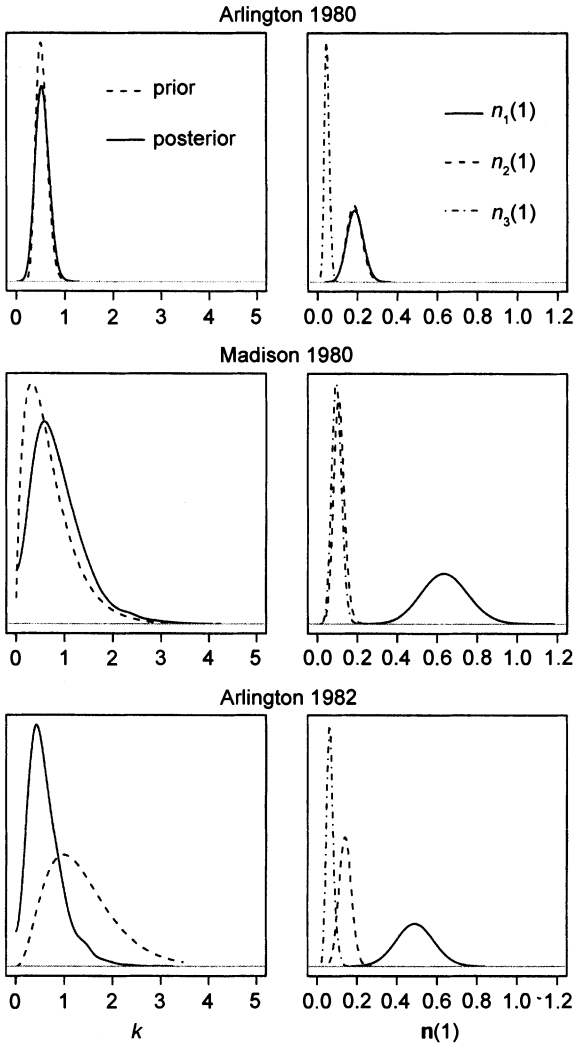


FIG. 6. Smoothed posterior densities for the aggregation parameter $k$ (left panels) and for the components of the initial density vector $\mathbf{n}(1)$ (right panels). Each row of panels corresponds to a different population. For $k$, the prior densities are also shown as dashed lines. The posterior densities for $n_1(1)$ and $n_2(1)$ from the Arlington 1980 population nearly coincide, as do the posteriors for $n_2(1)$ and $n_3(1)$ from the Madison 1980 population.

occasionally falling in the periphery of the high posterior density region. In all 25 simulations, the 95% posterior interval for $\lambda$ covered the true value (Fig. 9).

## DISCUSSION

### *Estimates of matrix parameters and model identifiability*

Three features of the posterior distribution of $\mathbf{A}$ stand out—strong negative correlations between matrix parameters sharing the same row of $\mathbf{A}$, substantial variability in the marginal posteriors for each of the matrix parameters, and little variability in the posterior distributions of $\lambda$ and $\mathbf{w}$. The first of these may be specific to the matrix parameterization chosen here, but the latter two typify the more general partial nonidentifiability problem that plagues inverse analyses (Wood 1997: 569). Essentially, when the matrix model fits well, the eventual dynamics of the system are determined by only $\lambda$ and $\mathbf{w}$, which are estimated precisely. However, because different demographic matrices can produce the same $\lambda$ and $\mathbf{w}$, the entire set of matrix parameters cannot be estimated knowing only $\lambda$ and $\mathbf{w}$ (Manly 1990:104–105, Wood 1994).

This being said, the transient dynamics at the beginning of each data series do provide some information about the matrix parameters beyond the information in $\lambda$ and $\mathbf{w}$, because they are determined by subdominant eigenvectors and eigenvalues, not just the dominant eigenvalue–eigenvector pair (Manly 1990). Consequently, not all parameter combinations that produce the same values of $\lambda$ and $\mathbf{w}$ are equally likely in the posterior. This explains why the matrix parameters are more precise for Arlington 1980 than for Madison 1980 (Fig. 2, Table 2). The Arlington 1980 population started further from its stable stage distribution, and so the transient dynamics were more prominent, providing more information about the subdominant eigenvalue–eigenvector pairs.

The negative correlations between matrix parameters sharing the same row of $\mathbf{A}$ can be explained by the characteristic equations for $\lambda$ and $\mathbf{w}$ generated by this particular matrix. Here, $\lambda$ and $\mathbf{w}$ are determined by

$$\left(\frac{F}{\lambda - P_1}\right)\left(\frac{G_1}{\lambda - P_2}\right)\left(\frac{G_2}{\lambda - P_3}\right) = 1 \qquad (7)$$

and

$$w_1 = \frac{F}{(\lambda - P_1)}$$

$$w_2 = \frac{F}{(\lambda - P_1)}\frac{G_1}{(\lambda - P_2)}$$

$$w_3 = \frac{F}{(\lambda - P_1)}\frac{G_1}{(\lambda - P_2)}\frac{G_2}{(\lambda - P_3)}(=1). \qquad (8)$$

where $w_i$ is the $i$th component of $\mathbf{w}$ (Caswell 2001: Section 7.3). Thus, the eventual dynamics of the matrix model are determined by the three quantities $F/(\lambda - P_1)$, $G_1/(\lambda - P_2)$, and $G_2/(\lambda - P_3)$. Clearly, then, estimates of $P_1$ and $F$ will be negatively correlated, because a decrease in the estimate of $F$ accompanied by an increase in the estimate of $P_1$ will leave $F/(\lambda - P_1)$ unchanged (assuming the change in $\lambda$ is negligible), and vice versa. The same holds for $(G_1, P_2)$ and $(G_2, P_3)$.

We cannot easily explain the bimodality of the posterior distribution for Arlington 1982. Numerical exploration of the posterior convinces us that the bimodality is indeed real, and not caused by a computational problem. Clearly, different combinations of vital rates could explain the data equally well, but why the pos-

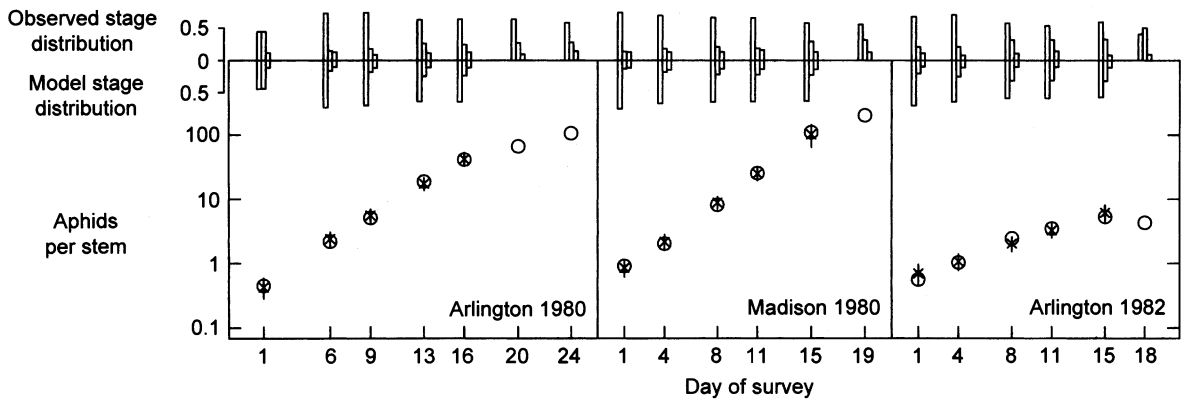


FIG. 7. Observed and fitted aphid population dynamics. Circles show the observed average number of aphids per stem, ×'s show posterior predictive means, and vertical line segments cover 95% posterior predictive intervals. Bar graphs at the top show observed (above the zero line) and posterior predictive mean (below the zero line) stage distributions. The left, middle, and right bars of each triple show the proportion of young juveniles, old juveniles, and adults in the sample, respectively.

terior distribution occupies two distinct modes as opposed to a unimodal band (such as the 1980 populations) is not apparent to us. Biologically, the indeterminacy is reasonable enough: slowly growing populations can be attributable to either high survival and long development times, or low survival and rapid development.

### *Biological insight*

Although we cannot precisely estimate the entire demographic matrix **A**, we can still draw some conclusions about the demography of these pea aphid populations. First, all three populations were growing at different rates (witness that the posterior intervals for $\lambda$ do not overlap; Table 2), with the Madison 1980 population growing most quickly and the Arlington 1982 population growing most slowly. At the stable stage distributions of these populations, young juveniles would have comprised over half the population, with older juveniles less abundant and adults less abundant still. The Arlington 1982 population's stable stage distribution had more older juveniles and fewer younger juveniles than either of the 1980 populations. These results about $\lambda$ and **w** are suggested by the data (Fig. 7), so it is reassuring that they also appear in the posterior distributions.

We can also draw a few conclusions about the average vital rates for pea aphids, within the limits of the identifiability constraints. In all populations, the posterior probabilities that $G_1 > P_1$ and $G_2 > P_2$ were large (99% and 100%, 94% and 98%, and 90% and 85% for Arlington 1980, Madison 1980, and Arlington 1982, respectively), suggesting that juveniles were developing rapidly. Additionally, there is 99% posterior probability that adult survival was less than either juvenile survival ($G_1 + P_1 > P_3$ and $G_2 + P_2 > P_3$) for the Arlington 1980 population, although evidence of the same for the other two populations is weaker (posterior probabilities of 73% and 74% for Madison 1980 and Arlington 1982, respectively). In all three populations, posterior distributions for adult fecundities were not far from the reproduction rates of 6–7 aphid nymphs per day observed in insectaries and greenhouses (Hutchison and Hogg 1984; A. R. Ives, *personal communications*), suggesting that field conditions do not lower reproduction rates much. The most striking difference between the Arlington 1982 vital rate estimates and those for the 1980 populations is that survival of large juveniles ($P_2 + G_2$) was markedly smaller for Arlington 1982. This suggests that a natural enemy (e.g., a predator, parasitoid, or fungal infection) was responsible for the retarded rate of population growth in the Arlington 1982 population, because it is less likely that an abiotic factor such as climate would have selectively reduced survival of one life stage.

Matrix sensitivities revealed substantial evidence that $\lambda$ was more sensitive to the growth rate of young nymphs than to the growth rate of older nymphs in both of the 1980 populations, but the opposite was true in the Arlington 1982 population. From a pest control perspective, this suggests that when aphid populations are growing rapidly, management strategies that reduce the survival of young nymphs will be most effective, but when the survival of older nymphs is already low, reducing old nymph survival even further will be more effective. Thus, the relative efficacy of pest control measures will depend on the background biotic and abiotic conditions.

All of these results were robust to the choice of a noninformative prior, although the degree of confidence that we can place in statements about **w**, **A**, and the matrix sensitivities depends on the assumption of multinomial variability in the stage-category data. In general, relaxing this assumption did not change the direction of our qualitative conclusions, but it did weaken their posterior support. For example, the posterior

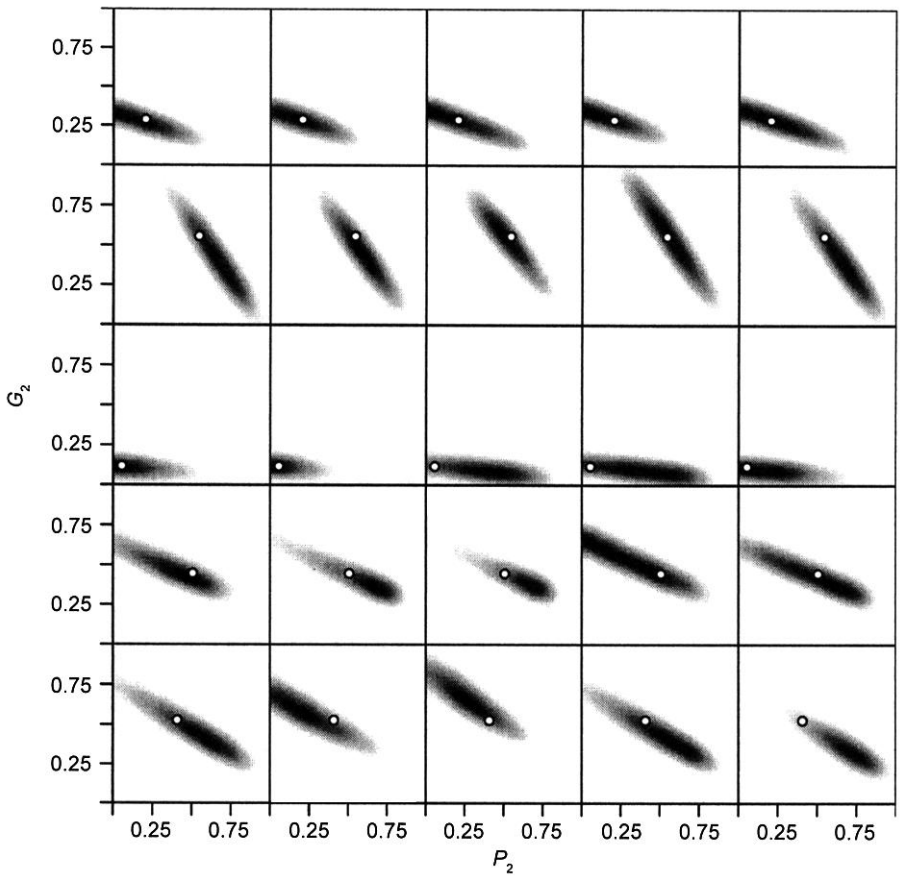


FIG. 8. Estimated bivariate posterior densities for matrix parameters $G_1$ and $P_2$ from 25 simulated data sets. White circles show values of the parameters used to generate the data. Each row shows five different simulations from the same set of parameter values. Darker regions indicate greater posterior density.

probabilities that $\partial\lambda/\partial G_1 > \partial\lambda/\partial G_2$ were 73%, 69%, and 17% for Arlington 1980, Madison 1980, and Arlington 1982, respectively, with the multinomial assumption relaxed. Posterior inference about $\lambda$ was robust to relaxing the multinomial assumption.

### *Model assumptions, validation, and possible violations*

Our model makes several assumptions. In particular, we assumed that a stage-structured matrix model with constant vital rates was appropriate for the modeled dynamics, that the negative binomial and multinomial models appropriately described the probability distribution of the observations (Eqs. 3–4), and that data from the same and different surveys were conditionally independent (Eq. 5). We examined the first two of these assumptions by comparing posterior predictive distributions to the observed data, and we examined the consequences of relaxing the multinomial assumption for the stage-categorized data.

With one exception, the posterior predictive distributions and the data agree. However, this agreement provides less evidence to validate our model assumptions than first meets the eye. Posterior predictive distributions are most useful when calculated for components of the data set that are auxiliary to the information used to estimate model parameters (Gelman et al. 1995: Chapter 6). Unfortunately, no such data were available to us, and in fact, the data to which the posterior predictives are compared contain nearly all the information used to estimate the parameters' posterior distribution. Nonetheless, our model is not so flexible that agreement between posterior predictives and data is guaranteed in advance, so the concordance between posterior predictives and data does provide some assurance that the model assumptions are appropriate (at least there is no evidence that the model assumptions are inappropriate), and is perhaps the best validation we can offer with the data available.

The one instance where posterior predictives did indicate some model shortcoming involved the Arlington 1982 population, where observed sample variances fell below the posterior predictive intervals in three of five cases. This suggests that aphids were not as aggregated among stems as the posterior for $k$ implies. We suspect this discrepancy was caused by a minor failure of the matrix model to match the observed dynamics. This failure generated larger differences between observed

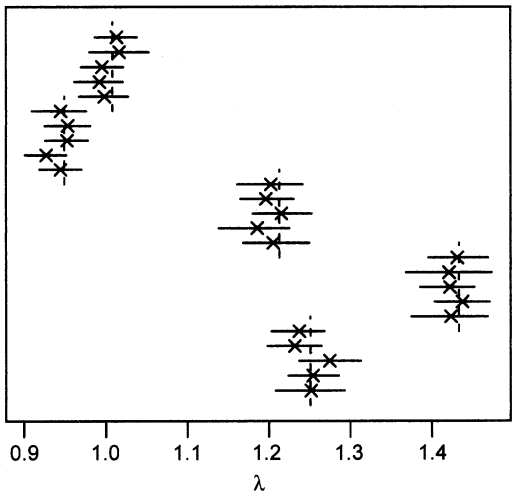


FIG. 9. Estimated posterior means and 95% posterior intervals for the population multiplication rate, λ, from 25 simulated data sets. Each horizontal line spans the 95% posterior interval for a single simulation, and the × marks the posterior mean. Dashed vertical lines show the true values of λ.

and predicted aphid densities, which the model accommodated by sending $k$ to smaller values, making more extreme observations more likely. This highlights the difficulty in interpreting $k$ directly. Because $k$ absorbs any variation in stem counts that is not accounted for by the matrix model, it subsumes both deviations from modeled dynamics and aggregation of aphids among stems.

The multinomial model for the stage-categorized data (Eq. 4) assumes that the stages of all aphids collected are conditionally independent given the true stage structure of the population. This is an assumption of convenience, and has been shown to be inappropriate in age-structured data from other systems (Methot 1990). In this case, we have reason to argue both for and against the appropriateness of this assumption. On one hand, pea aphids' habit of larvipositing young nymphs in groups and the limited mobility of juveniles make it more likely that young juveniles will be found together. On the other hand, by balancing collection effort among different sectors of each field, the sampling protocol made conditional independence among collected aphids more likely. In any case, our fit with a Dirichlet-multinomial model that allowed for dependence between collected aphids suggested that posterior inference for λ was robust to the multinomial assumption, as were posterior point estimates for $\mathbf{w}$. Posterior intervals for $\mathbf{w}$ and posterior distributions for $\mathbf{A}$ were sensitive to the multinomial assumption, although the posterior estimates for $\mathbf{w}$ were still moderately precise. These results make sense, given that the stage-structure data did not contain information about λ, but did inform the estimation of $\mathbf{w}$ and consequently $\mathbf{A}$.

Lastly, we note that if data from each of the sectors of the field had been available individually, we would have been in a better position to evaluate the observational distributions in Eqs. 3–4. Our experience provides an example of how information can be lost by retaining aggregate data instead of individual replicates.

### *Bayesian analysis, the inverse problem, and matrix estimation*

Although Bayesian statistics are gaining popularity in ecological use (e.g., Raftery et al. 1995, Ellison 1996, Link and Sauer 1996, Pascual and Kareiva 1996, Liermann and Hilborn 1997, Damgaard 1998), their place in ecological analyses is still a matter of (sometimes contentious) debate (Dennis 1996). The intent of this paper is not to champion one school of inference over the other on philosophical grounds. Indeed, with the exception of our empirical Bayes priors for $k$, the analyses presented here could also have been carried out in a frequentist context. However, the Bayesian approach can provide advantages in inverse problems and matrix estimation, in ways we note here.

First, informative priors can help resolve the partial nonidentifiability of inverse problems by introducing biological knowledge that discriminates among combinations of vital rates suggested by the observed dynamics. To illustrate, recall Wood's (1994) bear example. An informative prior on bear fecundity would deem a birth of 1 cub more likely than 100 cubs, helping to arbitrate between the possible combinations of vital rates that could explain the data. Wood has suggested countering instability in vital rate estimates by placing smoothness constraints on vital rates in successive stages (Wood and Nisbet 1991, Wood 1994, 1997). The Bayesian approach can accommodate this strategy as well, by using a prior that makes small differences between vital rates in consecutive stages more likely than large ones. One area where Bayesian techniques have gained favor in handling inverse problems is fisheries stock assessment (e.g., McAllister et al. 1994, Schnute 1994, Meyer and Millar 1999, Sitar et al. 1999). There, some of the advantages that a Bayesian approach provides—namely the abilities to incorporate informative priors and to make explicit the uncertainty in parameter estimates from complex models—are similar to those we realize here (Punt and Hilborn 1997, Quinn and Deriso 1999).

Second, the parameters of a transition matrix are rarely estimated from a single data set. Instead, estimates of matrix parameters are usually cobbled together from a variety of sources (e.g., Werner and Caswell 1977, Crouse et al. 1987, Fuller 1990, Doak et al. 1994, Wall et al. 1999), making statistical inference on functions of the matrix, such as λ and $\mathbf{w}$, difficult. In these cases, a Bayesian approach provides a way to estimate some parameters from data while incorporating information from other studies into the prior. (Though all our data came from the same study, this is similar to the approach we used to include infor-

mation about $k$.) Importantly, the informative prior can accommodate estimates of both the parameter estimates and their uncertainties, instead of forcing uncertainty in prior estimates to be ignored. The resulting joint posterior density of the matrix parameters can then be mapped into posterior densities for $\lambda$, $\mathbf{w}$, or other matrix functions, such as matrix sensitivities. These posteriors allow the modeler to understand how uncertainty in matrix parameters produces uncertainty (or certainty) in matrix functions.

### *Deterministic vs. stochastic matrix models*

Finally, we note that within this modeling framework, one could make the matrix model stochastic as well, introducing "process error" as well as "observation error." That is to say, the deterministic relationship $\mathbf{n}(t + 1) = \mathbf{A}\mathbf{n}(t)$ could be replaced by a stochastic model, where $\mathbf{n}(t + 1)$ is a random vector with a distribution determined by $\mathbf{A}$, $\mathbf{n}(t)$, and some random noise. We used a deterministic matrix model here because the near linearity of the mean abundances on a log scale suggest that a more complicated model with process error is not necessary. However, with data that do warrant process error models, a stochastic term could be added to the matrix model, moving the model into the realm of "state-space" models (Aoki 1987, Harvey 1989). State-space models can be analyzed using either Bayesian (Schnute 1994) or frequentist (de Valpine and Hastings 2002) methods.

### Acknowledgments

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## APPENDIX

Information on Bayesian estimation of a demographic matrix model from stage-frequency data is available online in ESA's Electronic Data Archive, *Ecological Archives* E083-060-A1.