
Stochastic Dynamic Northern Corn Rootworm Population Model

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Abstract

A complete life cycle model for northern corn rootworm, *Diabrotica barberi* Smith and Lawrence, is developed using a published single-season model of adult population dynamics and data from field experiments. Temperature-dependent development and age-dependent advancement determine adult population dynamics and oviposition, while a simple stochastic hatch and density-dependent larval survival model determine adult emergence. Dispersal is not modeled. To evaluate the long-run performance of the model, stochastically generated daily air and soil temperatures are used for 100-year simulations for a variety of corn planting and flowering dates in Ithaca, NY, and Brookings, SD. Once the model is corrected for a bias in oviposition, model predictions for both locations are consistent with anecdotal field data. Extinctions still occur, but these may be consistent with northern corn rootworm metapopulation dynamics.

Key words: Corn planting, corn rootworm, *Diabrotica barberi*, metapopulation dynamics, northern corn rootworm, oviposition.

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Introduction

Corn rootworm is the worst insect pest of corn in the United States, annually causing an estimated expense of \$1 billion in lost yields and control expenditures (Metcalf 1986). Northern corn rootworm, *Diabrotica barberi* Smith and Lawrence, and western corn rootworm, *Diabrotica virgifera virgifera* LeConte, are the species of economic concern in the primary corn-growing regions of the United States. Throughout the region, the western corn rootworm is generally the more problematic species; but the northern corn rootworm persists, and in areas such as New York and South Dakota it predominates (Naranjo and Sawyer 1989a, Ellsbury et al. 1998).

Recent developments have renewed interest in corn rootworm population modeling. Both northern and western corn rootworm have adapted to common corn rotations to become problems even in first-year corn, and the prevalence of this adaptation is spreading. Recent passage of the Food Quality Protection Act may lead to severe restrictions or banning of organophosphate and carbamate insecticides commonly used to control corn rootworm (US EPA 1999). Several seed companies are currently field testing transgenic corn that is resistant to corn rootworm, and resistance management strategies will be part of the registration process (Information Systems 1999).

Mooney and Turpin (1976) created a full life cycle model for corn rootworm but did not differentiate between northern and western corn rootworm. Hein and Tollefson (1987) and Elliot and Hein (1991) developed single-season models for western corn rootworm, while Naranjo and Sawyer (1989a) created a single-season model for northern corn rootworm. These single-season models were estimated and calibrated with observed air and soil temperatures from only a few years. Their long-run performance has not been evaluated under the wide variety of weather conditions possible at the locations for which they were parameterized or for other locations. This paper develops a complete life cycle model for northern corn rootworm and evaluates its long-run performance with simulated daily air and soil temperatures for Ithaca, NY, and Brookings, SD.

Materials and Methods

The single-season model of Naranjo and Sawyer (1989a) with slight modifications serves as the model of adult northern corn rootworm population dynamics from emergence to oviposition. A simple stochastic model predicts the percentage of eggs that hatch. Data from experiments described in Riedell et al. (1996) are used to develop a density-dependent model for larval survival to emergence.

Observed daily maximum and minimum air and soil temperatures from a few years are not used. Rather, stochastically generated daily air and soil temperatures that accurately capture the full range of potential weather exhibited by historical data are used to evaluate the long-run performance of the model. Daily air temperature generation is based on the method of Richardson (1981) and soil temperature generation is based on a modification of the method of Potter and Williams (1994). A first-order Markov chain with two stages (wet or dry) determines each day's precipitation status and an exponential model determines rainfall. Daily maximum and minimum air temperatures follow a lag one autocorrelated time series with lag zero and lag one cross-correlation and a mean and variance depending on each day's precipitation status. Soil temperatures depend on air temperatures but follow a lagged process due to soil heat storage and other factors. Mitchell (1999) provides a complete description of the method of weather generation. The result is a series of stochastically generated daily air and soil temperatures that accurately captures the full range of potential weather exhibited by historical data.

Naranjo and Sawyer (1989a) presented their model in continuous time but actually implemented it with a discrete time step of one day. The model here is presented in discrete form as implemented with a half-day time step. Following Naranjo and Sawyer (1989a), the first half day lasts 15 hours, from the current day's maximum to the next day's minimum (2:00 PM to 5:00 AM for air, 4:00 PM to 7:00 AM for soil). The second half day lasts 9 hours from the current day's minimum to the current day's maximum.

Adult Population Dynamics

Adult stage population dynamics are adapted from Naranjo and Sawyer (1989a):

$$P_{c,t}^{ImmF} = \begin{cases} E_t^{ImmF} & \text{if } c = 1 \\ P_{c,t-1}^{ImmF} (1 - k_t M_t) (1 - k_t A_{c,t}^{ImmF}) & \text{if } c > 1 \end{cases} \quad (1)$$

$$P_{c,t}^{MatF} = \begin{cases} \sum_{c=1}^{C_t^{ImmF}} [P_{c,t}^{ImmF} (1 - k_t M_t) (k_t A_{c,t}^{ImmF})] & \text{if } c = 1 \\ P_{c,t-1}^{MatF} (1 - k_t M_t) (1 - k_t A_{c,t}^{MatF}) & \text{if } c > 1 \end{cases} \quad (2)$$

$$P_{c,t}^{Post} = \begin{cases} \sum_{c=1}^{C_t^{MatF}} [P_{c,t}^{MatF} (1 - k_t M_t) (k_t A_{c,t}^{MatF})] & \text{if } c = 1 \\ P_{c,t-1}^{Post} (1 - k_t M_t) & \text{if } c > 1 \end{cases} \quad (3)$$

$$P_{c,t}^{Male} = \begin{cases} E_t^{Male} & \text{if } c = 1 \\ P_{c,t-1}^{Male} (1 - k_t M_t) & \text{if } c > 1. \end{cases} \quad (4)$$

$P_{c,t}^s$ is the adult population (m^{-2}) in life stage s , in cohort c , during time period t . Life stage s is *ImmF* for immature female, *MatF* for mature female, *Post* for post-reproductive female, and *Male* for male. Cohorts range in number between 1 and C_t^s for each stage, with the number C_t^s varying depending on the time period. When a new cohort advances to the next stage, it starts as cohort $c = 1$, and all existing cohorts have their index c incremented by one. The time period t is $n1$ for the first half day and $n2$ for the second half day of day n . Lastly, k_t converts variables from days to half days: $k_t = 15/24$ for $t = n1$ and $k_t = 9/24$ for $t = n2$, since the respective half days last 15 and 9 hours.

In Equations (1) and (4), E_t^s is the number of adults of stage s emerging during time step t to become the new first cohort. The summations in Equations (2) and (3) determine the number of adults advancing to the next stage to become the new first cohort. M_t is the daily proportional mortality rate and $A_{c,t}^s$ is the probability that members of cohort c advance during time period t .

Unlike Naranjo and Sawyer's (1989a) model, dispersal is not included despite its obvious importance in corn rootworm population dynamics. Estimating dispersal as the residual between predicted and observed populations ignores the age and reproductive status of entering individuals and does not permit generalization over space and time. However, data were not available to develop a mechanistic model. As a result, this model is for a regional population for which dispersal is insignificant.

Emergence

Naranjo and Sawyer (1989a) estimated functions for male and female emergence:

$$E_t^s(g_t) = \frac{E_{Total}^s}{g_t \mathbf{s}_E^s \sqrt{2\mathbf{p}}} \exp\left[-\frac{(\ln(g_t) - \mathbf{m}_E^s)^2}{2\mathbf{s}_E^{s^2}}\right] (g_t - g_{t-1}) \quad (5)$$

E_{Total}^s is the total number of males ($s = Male$) or females ($s = ImmF$) emerging and is determined from E_{Total} , the total number emerging. The larval survival model provides E_{Total} and the proportion of E_{Total} that is female is $-0.15 + 0.00080x$, where x is the sum of soil degree days with a base of 10°C accumulated from March 1 to the plant date and air degree days with a base 10°C accumulated from the plant date to the day of peak flower.

In Equation (5), g_t is time measured in accumulated soil degree days with a base of 10°C from March 1, and \mathbf{m}_E^s and \mathbf{s}_E^s are the mean and standard deviation of emergence times on a natural logarithm scale for the specified stages. Using x as previously defined,

$$\mathbf{m}_E^{Male} = \ln(547.88 + 0.39x) \text{ and } \mathbf{m}_E^{ImmF} = \ln(800.85 + 0.24x), \text{ while } \mathbf{s}_E^{Male} = 0.0901 \text{ and } \mathbf{s}_E^{ImmF} = 0.0998.$$

Mortality

The daily proportional rate of mortality is

$$M_t(\mathbf{y}) = M_{Max} \exp(-f\mathbf{y}), \quad (6)$$

where y is the proportion of corn plants in flower, $M_{Max} = 0.143$ is the maximum proportional rate of mortality, and $f = 1.924$ determines the rate of decline in mortality as y increases. Use d , air degree days for a base of 10°C accumulated from the plant date, to determine y :

$$\mathbf{y} = \frac{1}{1 + \exp\left(-\frac{c2-d}{\sqrt{d}}\right)} - \frac{1}{1 + \exp\left(-\frac{c1-d}{\sqrt{d}}\right)}, \quad (7)$$

where $c1 = -2.57 + 0.86y$, $c2 = 127.51 + 0.97y$, and y is the air degree days for a base of 10°C accumulated from planting date to the day of peak flower.

Advancement

In Equations (2) and (3) $A_{c,t}^s$, the probability that females in cohort c and stage s advance to the next stage during time period t , depends on $a_{c,t}^s$, the physiological age of the individuals in cohort c and stage s during time period t :

$$A_{c,t}^s(a_{c,t}^s) = \frac{F^s(a_{c,t}^s) - F^s(a_{c,t-1}^s)}{1 - F^s(a_{c,t-1}^s)}. \quad (8)$$

$F^s(a)$ is the distribution function of stage s evaluated at age a , determined by defining $z = (V - a)/(V - U)$ and $w = z^q$:

$$F^s(a) = \begin{cases} 0 & \text{if } a < U^s \\ (1 - z)^{wq} & \text{if } U^s < a < V^s \\ 1 & \text{if } a > V^s \end{cases}. \quad (9)$$

Values for U , V , q , and q are $U^{ImmF} = 0.4710$, $U^{MatF} = 0.0999$, $V^{ImmF} = 2.0300$, $V^{MatF} = 2.8917$, $q^{ImmF} = 1.0263$, $q^{MatF} = 1.2483$, $q^{ImmF} = 1.1706$, and $q^{MatF} = 0.5471$.

The physiological age of females in a cohort is determined by integrating the development rate function of the stage from the time individuals enter a stage. The development rate function depends on the temperature (T) and stage-specific parameters. For immature females:

$$r(T) = \frac{T(R/298.15)\exp[(HA/1.987)((1/298.15) - (1/T))]}{1 + \exp[(HH/1.987)((1/TH) - (1/T))]}, \quad (10a)$$

where T is temperature in Kelvin, $R = 0.1081$, $HA = 13158.39$, $HH = 58016.57$, and $TH = 302.85$. For mature females, $R = 0.0358$ and $HA = 10988.04$ and

$$r(T) = T(R/298.15)\exp[(HA/1.987)((1/298.15) - (1/T))]. \quad (10b)$$

A sine function interpolates hourly temperatures between maximum and minimum temperatures. Denote the amplitude as $\mathbf{a} = \frac{1}{2}(T_{Max} - T_{Min})$ and the period as $p = 2(h_{End} - h_{Begin})$, then for

hour h , $T(h) = T_{Avg} + \mathbf{a} \sin\left(\frac{2\mathbf{p}}{p}(h - h_{Begin} + k_{ni}p)\right)$, where T_{Avg} is the average of the maximum

and minimum and $k_{n1} = 0.75$ and $k_{n2} = 0.25$.

An hourly time step is used to approximate the integral of the rate function $r(T)$ with a summation technique. The average development rate for any two subsequent hours h_j and h_{j+1} is

$r_{Avg}(h_j) = \frac{1}{2}(r(T(h_j)) + r(T(h_{j+1})))$. Aging that occurs during any half-day time period t is

$\mathbf{g} = \frac{1}{24} \sum_{h_j=h_{Begin}}^{h_{End}} r_{Avg}(h_j)$, where $h_{Begin} = 14$ for $n1$ and 5 for $n2$, and $h_{End} = 29$ for $n1$ and 14 for $n2$.

The age of any cohort c of stage s during any time period t is the sum of all \mathbf{g} from the time period when the cohort began (t_{Begin}) until the current time period t : $a_{c,t}^s = \sum_{t=t_{Begin}}^t \mathbf{g}$.

Oviposition

Using notation as in (1) – (4), the total number of eggs oviposited by mature females in cohort c in time period t is:

$$P_{c,t}^{Eggs} = \begin{cases} \sum_{c=1}^{C_t^{MatF}} [O(a_{c,t}^{MatF}) P_{c,t}^{MatF}] & \text{if } c = 1 \\ P_{c,t-1}^{MatF} + \sum_{c=1}^{C_t^{MatF}} [O(a_{c,t}^{MatF}) P_{c,t}^{MatF}] & \text{if } c > 1, \end{cases} \quad (11)$$

where $O(a)$ is the age-dependent oviposition function. Total oviposition for the season is:

$$P_{Total}^{Eggs} = \sum_{t=1}^{365} \sum_{c=1}^{C_t^{MatF}} O(a_{c,t}^{MatF}) P_{c,t}^{MatF} . \quad (12)$$

The age-dependent oviposition function $O(a)$ is:

$$O(a_t, T) = \frac{f(T)}{s_o^s \sqrt{2\mathbf{p}}} \exp\left[-\frac{(a_t - m_o^s)^2}{2s_o^s{}^2}\right] (a_t - a_{t-1}) , \quad (13)$$

where a_t is the age of the mature female cohort, $m_o = 1.1222$, and $s_o = 0.6996$. The fecundity function $f(T)$ is the same as Equation (10a), except $R = 776.55$, $HA = 12249.96$, $HH = 64747.54$, and $TH = 300.52$.

Hatch

Woodson and Ellsbury (1994) develop a predictive model of egg mortality that is not usable for eggs exposed to varying temperatures. Woodson et al. (1996) estimate a model of egg development under varying temperatures but do not include mortality. As a result, a simple model of egg hatch is used. The percentage of eggs that hatch is normally distributed with a mean of $m_h = 50$ percent and a standard deviation $s_h = 8$ percent, implying that the percent hatch is between 30 percent and 70 percent in almost 99 percent of the years. For comparison, Woodson and Ellsbury (1994) report hatch rates from 5 percent to 68 percent for eggs exposed to 16 weeks of different constant temperature treatments between 0°C and -10°C in the laboratory. Woodson et al. (1996) report average hatch rates of 56 percent to 81 percent in the laboratory for eggs collected from feral females near Brookings and chilled at 8°C for 6–9 months. Fisher (1989) reports 58 percent (± 12 percent) and 62 percent (± 11 percent) for western corn rootworm eggs exposed to field conditions over the winter and hatched in the field and in the laboratory, respectively.

Once the percentage of larvae that hatch (H) is determined, the initial larval population (P^{Larvae}) is the proportion of the previous year's total egg population (P^{Eggs}_{Total}) that hatches:

$$P^{Larvae} = 0.01HP^{Eggs}_{Total}.$$

Larval Survival

Existing models of northern and western corn rootworm larval development do not account for mortality (Jackson and Elliot 1988, Woodson and Jackson 1996), while published research on density-dependent survival of northern and western corn rootworm larvae to emergence does not include models (Elliot et al. 1988, Woodson 1994). As a result, the proportion of larvae surviving to emerge as adults is estimated with field data from three years of artificial infestation experiments with western corn rootworm near Brookings, SD. See Riedell et al. (1996) for a description of the experiment and a summary of results. Western corn rootworm eggs with known percent hatch were placed in the soil to obtain three experimentally controlled initial larval populations (1200, 2400, and 4800 larvae m^{-1}). The respective mean hatch for each treatment was 5.17 percent (± 3.85 percent), 3.20 percent (± 1.92 percent), and 2.01 percent (± 1.16 percent).

Histograms in Figure 1 indicate that for a fixed larval population the proportion surviving is not normally distributed about the mean, nor is the variance constant. As a result, ordinary least

squares regression of survival on larval population for a linear or nonlinear specification is not appropriate. Instead of searching for a variance stabilizing transformation and a nonlinear specification, maximum likelihood with a non-normal error specification is used.

The beta distribution is sufficiently flexible to allow symmetric or skewed unimodal densities, as well as U- and J-shaped densities, and has lower and upper bounds of 0.0 and 1.0 (Evans et al. 1993). The beta density seems appropriate since the proportion surviving must be between 0.0 and 1.0 and the histograms show varying degrees of skewness. If v , the proportion of the initial larval population surviving to emergence, follows the beta distribution, its density function $b(v)$ is

$$b(v) = \frac{(v^{a-1}(1-v)^{w-1})\Gamma(a+w)}{\Gamma(a)\Gamma(w)}, \quad (14)$$

where Γ is the gamma function, and a and w are parameters to be estimated.

To capture the effect of population density as exhibited by the data, the parameter w is estimated as a linear function of the initial larval population: $w = w_0 + w_1 P^{larvae}$. The log-likelihood function is

$$\begin{aligned} \ln L(\mathbf{a}, \mathbf{w}_0, \mathbf{w}_1) = N & \left[\ln \Gamma(\mathbf{a} + \mathbf{w}_0 + \mathbf{w}_1 P^{larvae}) - \ln \Gamma(\mathbf{a}) - \ln \Gamma(\mathbf{w}_0 + \mathbf{w}_1 P^{larvae}) \right] \\ & + (\mathbf{a} - 1) \sum_{i=1}^N \ln(v_i) + (\mathbf{w}_0 + \mathbf{w}_1 P^{larvae} - 1) \sum_{i=1}^N \ln(1 - v_i), \end{aligned} \quad (15)$$

where $i = 1$ to N indexes observations of v , N is the total number of observations, and a , w_0 , and w_1 are parameters. Table 1 provides parameter estimates.

For the beta density with parameters a and w , the mean is $a / (a + w)$, and the standard deviation is the square root of $a w / ((a + w)^2 (a + w + 1))$ (Evans et al. 1993). Figure 2 plots the data and the observed and predicted means for each initial larval population, as well as the observed and predicted standard deviations for each initial larval population. The model closely follows the observed means and adequately describes the standard deviation.

The larval survival model can be deterministic or stochastic. For the deterministic case, the proportion of the initial larval population surviving to emergence is the mean of the density $b(v)$: $v = E[v] = \frac{2.83}{2.83 + 22.9 + 0.0246 P^{larvae}}$. For the stochastic case, the proportion of larvae surviving

to emergence is a random variable from a beta density with parameters $a = 2.83$ and $w = 22.9 + 2.46P^{larvae}$. To evaluate the model's long-run performance under the wide variety of conditions that can occur, the stochastic version of the model is used here.

Once v is determined, the total number of adults that emerge is $E_{Total} = vP^{larvae}$, which links the larval survival model to the adult population model to complete the corn rootworm life cycle.

Simulations

The model as described was programmed in C++ using Microsoft's Visual C++ compiler. Because corn phenology is an important determinant of corn rootworm population dynamics, 272 combinations of planting and peak flowering dates summarized in Table 2 were developed using dates reported in Naranjo and Sawyer (1988) and Riedell et al. (1996). Naranjo and Sawyer (1989b) note that their model is more sensitive to the day of peak flower than plant date, so the day of peak flowering is varied in one-day increments and plant date is varied in four-day increments.

For each combination, a 100-year simulation is run beginning on January 1 with an initial egg population (P_{Total}^{Eggs}) of 1000 for Ithaca, NY, and Brookings, SD. Because a population can become extinct in a stochastic model, if total oviposition is less than 10 eggs, the initial larval population the next year is calculated using 10 eggs. A different set of stochastic daily air and soil temperature data is generated for each simulation, and degree day calculations use Allen's (1976) method.

Results and Discussion

Long-Run Performance

Figure 3 provides a summary of the model's performance in Ithaca and Brookings. Each point is the average peak adult population or average annual oviposition (m^{-2}) from a 100-year simulation for one of the 272 combinations listed in Table 2. A simple rule to convert populations to a per plant basis is to divide by seven, assuming a density of 28,340 corn plants per acre. Thus Figure 3 shows that average populations never rise above 0.5 adults per plant. Figure 4 indicates that simulated populations in both locations rise above one adult per plant on average less than 4 out of 100 years. Most of these high population years occur during the initial years because the model begins with an egg population of 1000 eggs. As an example, Figure 5 illustrates annual

adult population dynamics for a 100-year simulation. The population may recover after its initial crash but cannot sustain itself.

The model does not predict a long-run sustainable population in either location. In almost all runs, the population quickly crashes to a relatively small number maintained by the minimum oviposition of 10 eggs artificially imposed on the model to prevent extinction. Figure 4 indicates that for early flowering corn, on average the oviposition minimum of 10 eggs is binding in over 95 percent of the years in both locations, while for late flowering corn the minimum is binding in about 65 percent of the years.

Corrected Model

In the evaluation of their model, Naranjo and Sawyer (1989a) note that the corn phenology and oviposition components performed the least adequately. The corn phenology model performed poorly on hybrids for which it had not been calibrated, but did not show a consistent error. The oviposition model consistently underpredicted observed oviposition, particularly when oviposition was low. Naranjo and Sawyer (1989b) found predicted oviposition particularly sensitive to the parameters determining the day of peak flower and the duration of flowering. By using a wide variety of plant day and day of peak flowering combinations and several years of weather data, the analysis here captures the effects of corn phenology on model performance.

The predicted oviposition error is so consistent that regressing observed oviposition (O_o) on predicted oviposition (O_p) yielded $O_o = 360 + 0.75O_p$, with $r^2 = 0.94$ for nine observations (Naranjo and Sawyer 1989a). As Figure 6 illustrates, this provides a relatively large increase at low levels of oviposition and a slight increase at higher levels. This error may explain the model's poor performance. In this stochastic model, a population eventually has some "bad" years and falls to relatively low levels. The population then has a difficult time recovering given the nature of the oviposition error.

Naranjo and Sawyer's (1989a) estimated correction imposes a minimum annual oviposition of 360 eggs, which seems excessive. To provide a relatively larger increase at low levels of oviposition and still pass through the origin, as well as use Naranjo and Sawyer's (1989a) estimated correction, a spline function is used to correct Equation (12):

$$\tilde{P}_{Total}^{Eggs} = \begin{cases} 1500(1 - \exp(-0.0013P_{Total}^{Eggs})) & \text{if } P_{Total}^{Eggs} \leq 585 \\ 0.75P_{Total}^{Eggs} + 360 & \text{if } 585 < P_{Total}^{Eggs} \leq 1440 \\ P_{Total}^{Eggs} & \text{if } P_{Total}^{Eggs} > 1440 \end{cases} \quad (16)$$

\tilde{P}_{Total}^{Eggs} is the new “corrected” total egg population at the end of the season and is used in place of P_{Total}^{Eggs} to determine P^{Larvae} . The spline follows a negative exponential rise until the original predicted oviposition intersects the correction equation estimated by Naranjo and Sawyer (1989a), then follows their equation until it intersects with the $P_{Total}^{Eggs} = \tilde{P}_{Total}^{Eggs}$ line. Figure 6 illustrates the spline correction equation and compares it with the equation estimated by Naranjo and Sawyer (1989a).

Long-Run Performance of the Corrected Model

Figure 7 illustrates the long-run performance of the corrected model. Average peak adult populations and annual oviposition rise considerably in both locations for corn with peak flowering occurring after Julian day 225 (August 13). Also, on average, Ithaca exhibits slightly larger populations and oviposition than Brookings. Figure 8 shows that the average proportion of years that simulated populations exceed one adult per plant increases approximately ten-fold. For corn with a late day of peak flowering, the percentage rises to almost 40 percent in Ithaca but remains fairly constant at almost 20 percent in Brookings.

The corrected model can sustain corn rootworm populations in the long run when the corn consistently has a late day for peak flower. Figure 8 indicates that in less than 10 percent of the years, corn with a peak flowering day after Julian day 235 (August 23) has a total oviposition less than 10 eggs m^{-2} in both locations, which is far fewer than in the original model. Figure 9 shows that the population can recover from very low levels when the corn consistently has a late day of peak flowering, but still exhibits long periods of relatively low populations.

The corrected model predicts peak adult populations that are comparable to field data. Figures from Naranjo and Sawyer (1989a) indicate peak adult populations near Ithaca of around 25 adults m^{-2} for an early flowering variety and around 35 adults m^{-2} for a late flowering variety. Figures from Lance et al. (1989) indicate peak adult populations of about 2.5 and 5 adults per plant for two locations in eastern South Dakota, or approximately 17.5 and 35 adults m^{-2} .

Mullock et al. (1995) report per plant peak adult populations for seven fields near Elora, Ontario. Two fields had 0.1, two had 0.2, and the other three fields had 0.7, 1.0, and 3.6 adults per plant. The corrected model predicts populations that are more typical of those reported by Mullock et al. (1995), but predictions consistent with the observations of Naranjo and Sawyer (1989a) and Lance et al. (1989) are common.

Discussion

The original model of Naranjo and Sawyer (1989a) did not produce sustainable populations in either Ithaca, NY, or Brookings, SD, apparently due to inadequate oviposition. Factors other than a problem with the oviposition model can lead to underpredicting oviposition. For example, the model of corn phenology may be inadequate and cause excessive mortality, or the mortality model may predict excessive mortality. Both would reduce adult populations and oviposition. The ad hoc spline function used to correct oviposition indicates that factors contributing to oviposition may be the area on which research should focus to create an improved model based on biological foundations. Extended diapause and multiple mating of females are not modeled but should improve model performance.

Simulation results with the corrected oviposition model indicate that a model based on environmental variables and estimated for one region can be used in another region. The temperature-dependant model of adult population dynamics performed well even though climate differences between Ithaca and Brookings are not small. For example, the average annual temperature in Ithaca is 8.0°C and in Brookings it is 6.2°C.

The population extinctions predicted by the original and corrected models may not be unrealistic. In standard metapopulation models, areas with large populations serve as sources that revitalize areas with declining populations or recolonize areas with extinct populations^{3/4}local populations may go extinct, but the metapopulation persists (Gotelli 1998). Ellsbury et al. (1998) demonstrate that extensive areas of corn fields can have locally extinct populations of northern corn rootworm (zero adult emergence), yet other parts have substantial populations. If the original or corrected model were put into a spatial context and explicitly incorporated the age and reproductive status of dispersing individuals, local extinctions could

still occur, but the model might create a sustainable metapopulation that is consistent with data such as that reported by Ellsbury et al. (1998). Spatially explicit stochastic dynamic metapopulation models of this sort have not been developed for corn rootworm to test this hypothesis.

Potential applications of the original or corrected models include the development and evaluation of alternative management strategies for corn rootworm based on manipulating corn phenology. Such strategies could be part of areawide management once the population has been suppressed, or they may become important if traditional insecticides become unavailable. Also the model could serve as the biological foundation for developing and evaluating resistance management strategies for traditional insecticides, transgenic crops, and rotational resistance.

Table 1. Parameter estimates for the conditional beta density function for larval survival

Parameter	Estimate	Standard Error^a	t Statistic	P Value
a	2.83	0.411	7.76	<0.001
w_0	22.9	7.13	2.56	0.01
w_1	0.0246	0.00544	4.85	<0.001

^a Computed according to the method of Berndt et al. (1974).

Table 2. Planting and peak flowering date combinations for which population model simulations are conducted

Plant Day	Peak Flower Range	Combinations
May 1	August 2 to August 25	24
May 5	August 2 to August 25	24
May 9	August 2 to August 25	24
May 13	August 2 to August 25	24
May 17	August 2 to September 2	32
May 21	August 2 to September 2	32
May 25	August 10 to September 2	24
May 29	August 10 to September 2	24
June 2	August 18 to September 2	16
June 6	August 18 to September 2	16
June 10	August 18 to September 2	16
June 14	August 18 to September 2	16

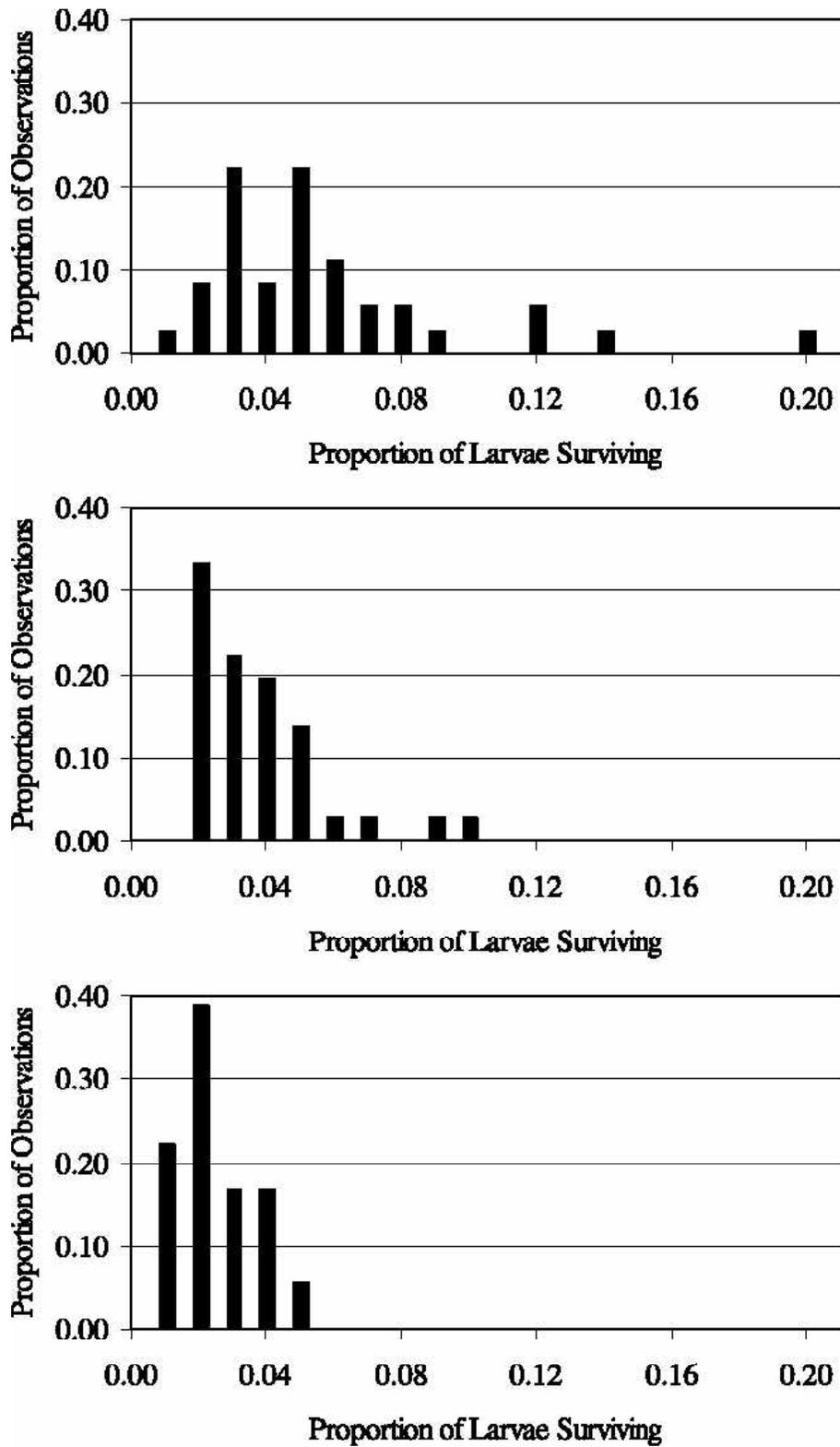


Figure 1. Histograms for proportion of larvae surviving to emergence for an initial larval population of 1200 (top), 2400 (middle), and 4800 (bottom) larvae per meter of row.

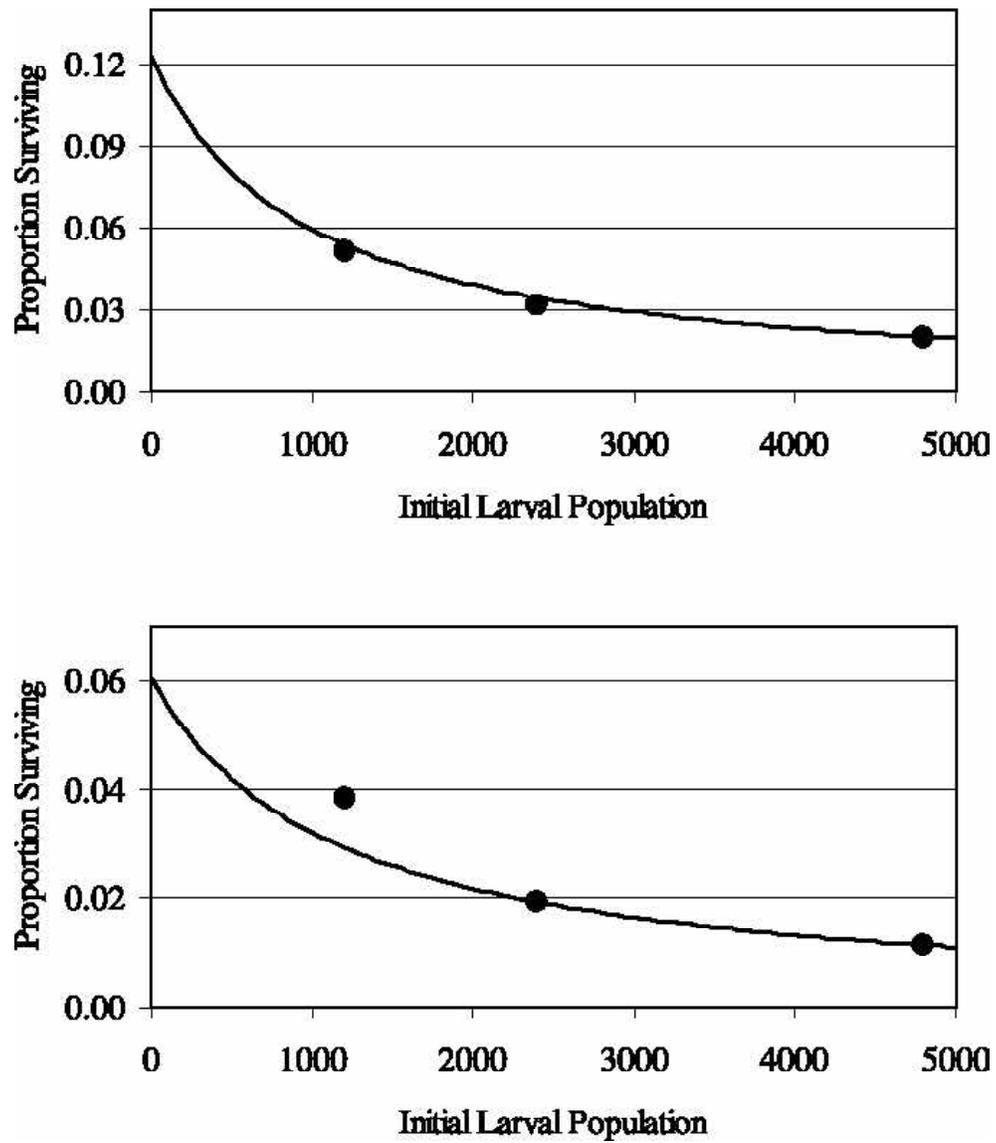


Figure 2. Observed (dots) and estimated (line) mean survival versus initial larval population (top). Observed (dots) and estimated (line) standard deviation of larval survival versus initial larval population (bottom).

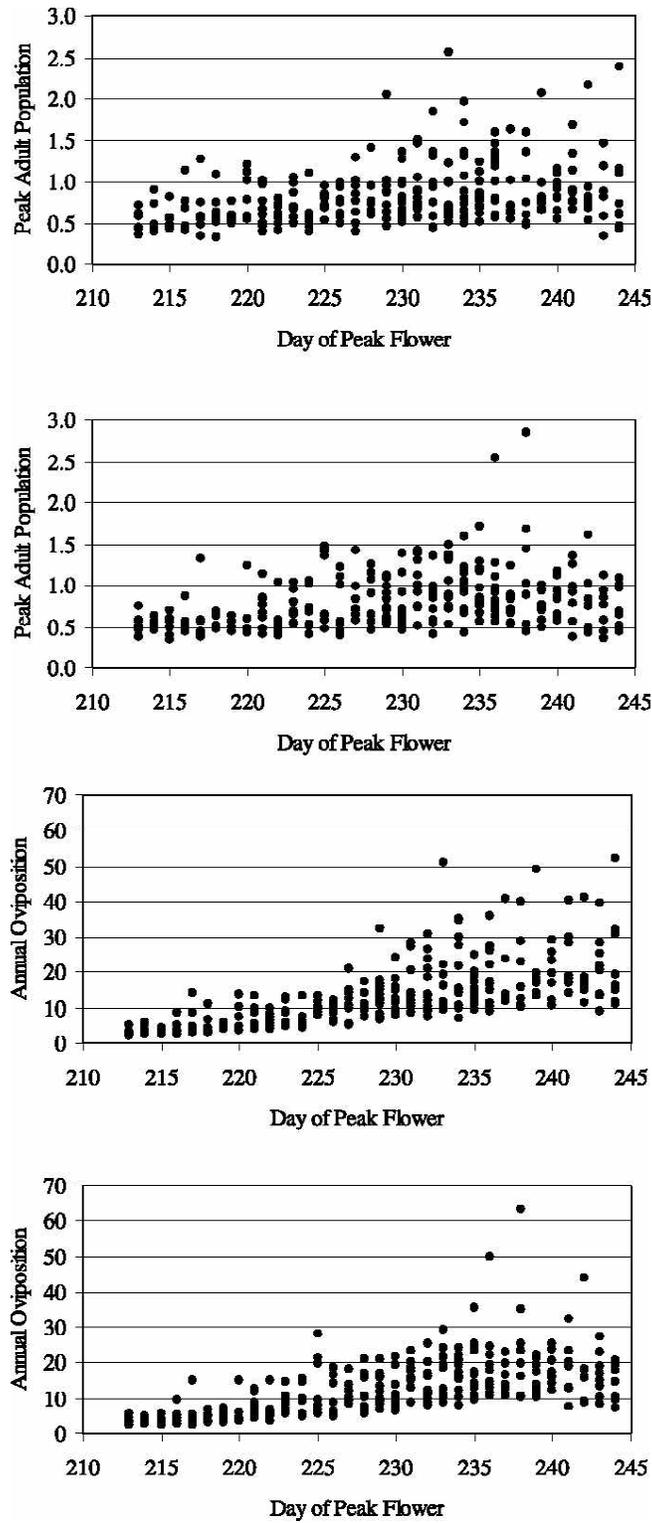


Figure 3. Simulated 100-year average peak adult population (m^{-2}) versus day of peak flower in Ithaca (top) and Brookings (bottom).

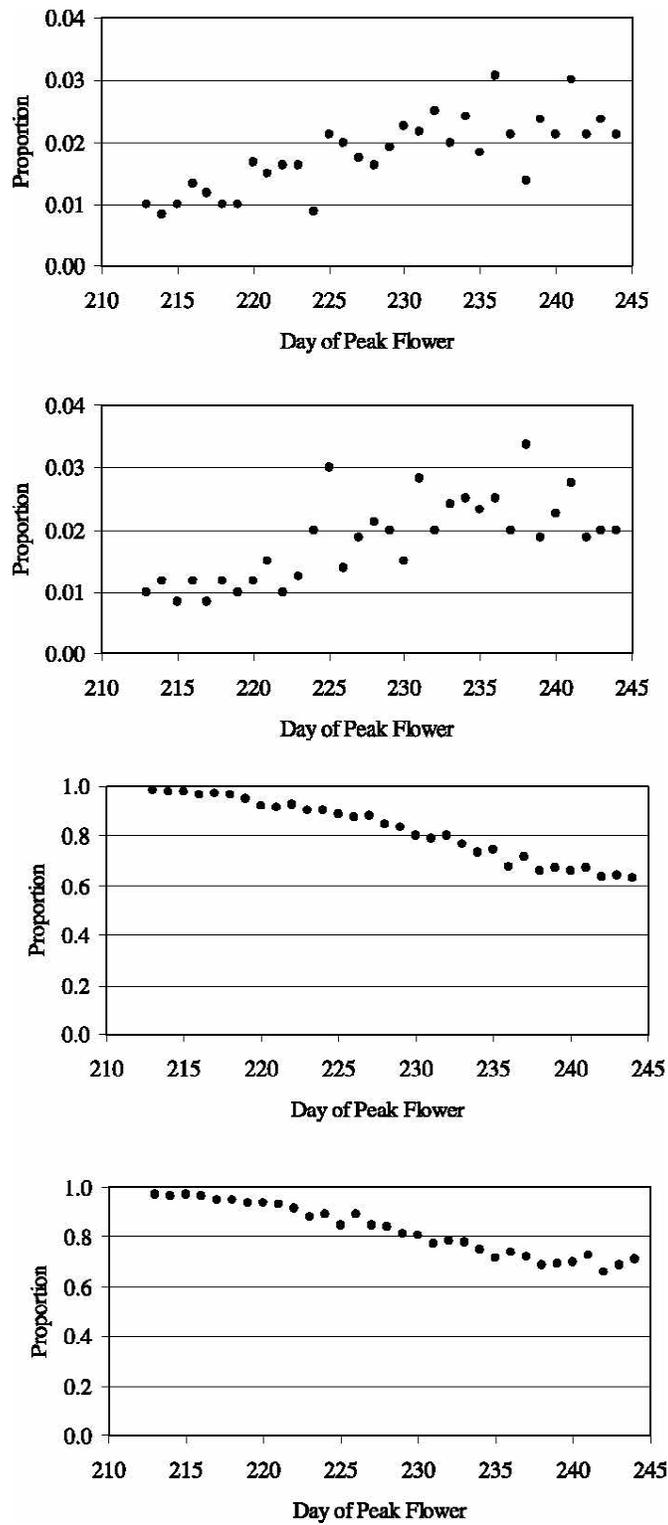


Figure 4. Average proportion of years that simulated peak adult population exceeds one adult per plant versus day of peak flower in Ithaca (top) and Brookings (bottom).

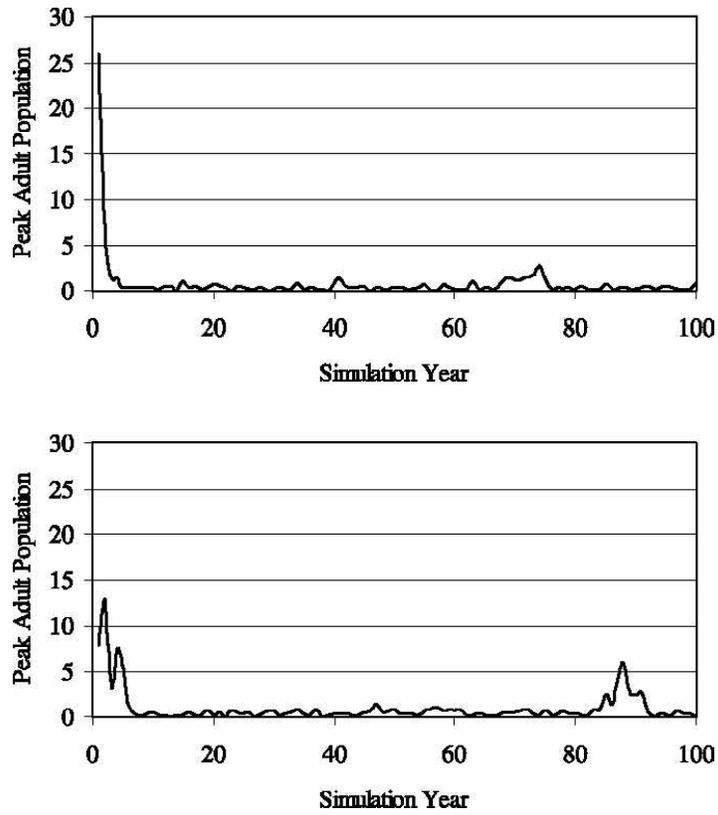


Figure 5. Annual time series of peak adult population (m^2) for a May 21 plant date and peak flower on August 29 in Ithaca (top) and Brookings (bottom).

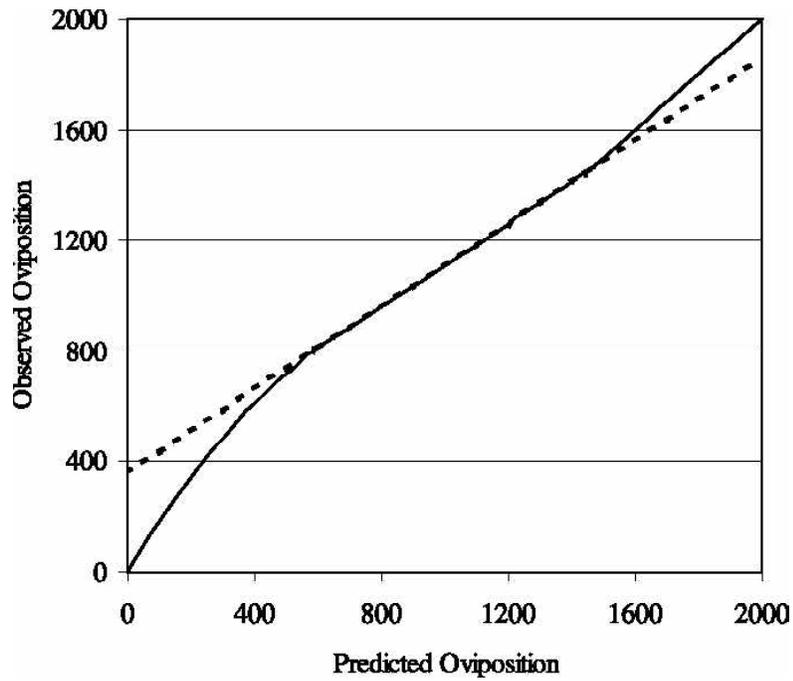


Figure 6. Spline function used to correct oviposition (solid line) and Naranjo and Sawyer's (1989a) linear correction function (dashed line).

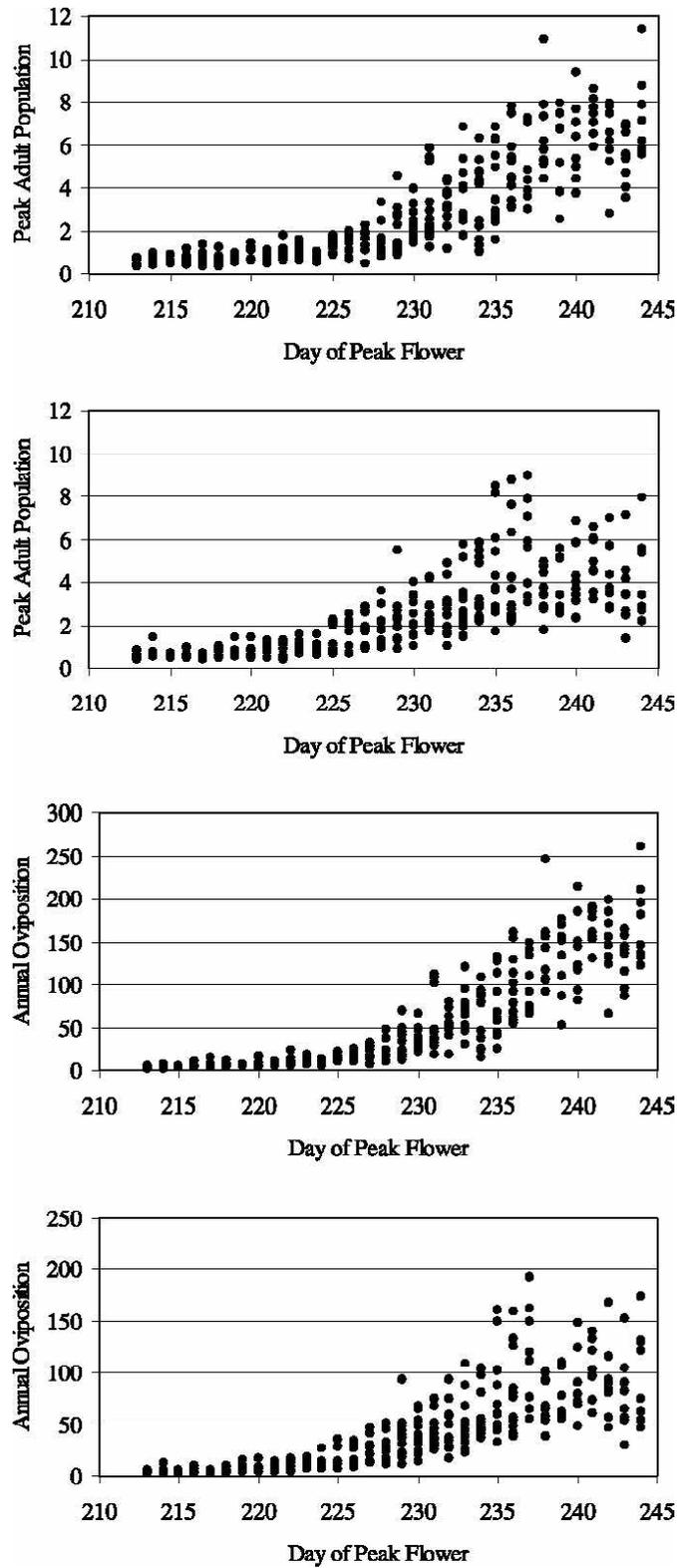


Figure 7. Simulated 100-year average peak adult population (m^{-2}) for the corrected model versus day of peak flower in Ithaca (top) and Brookings (bottom).

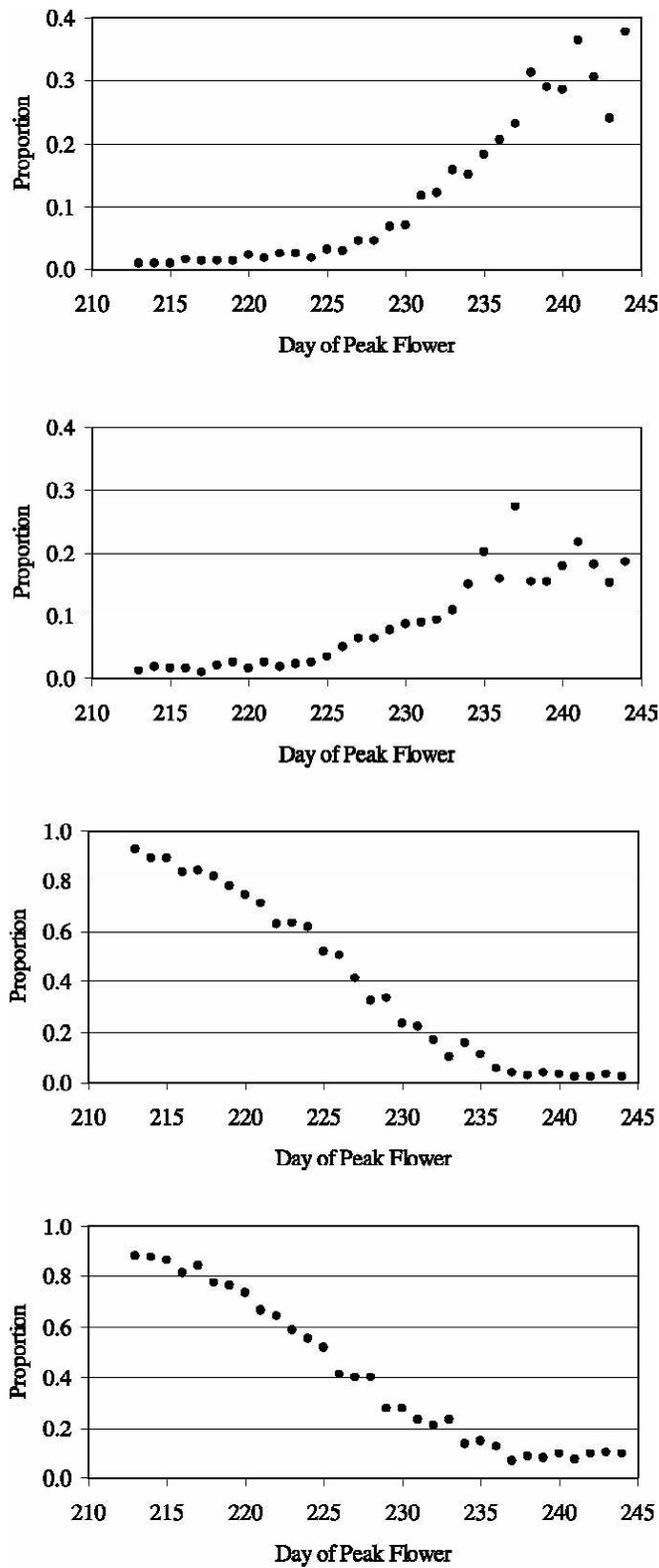


Figure 8. Average proportion of years that simulated peak adult population in corrected model exceeds one adult per plant versus day of peak flower in Ithaca (top) and Brookings (bottom).

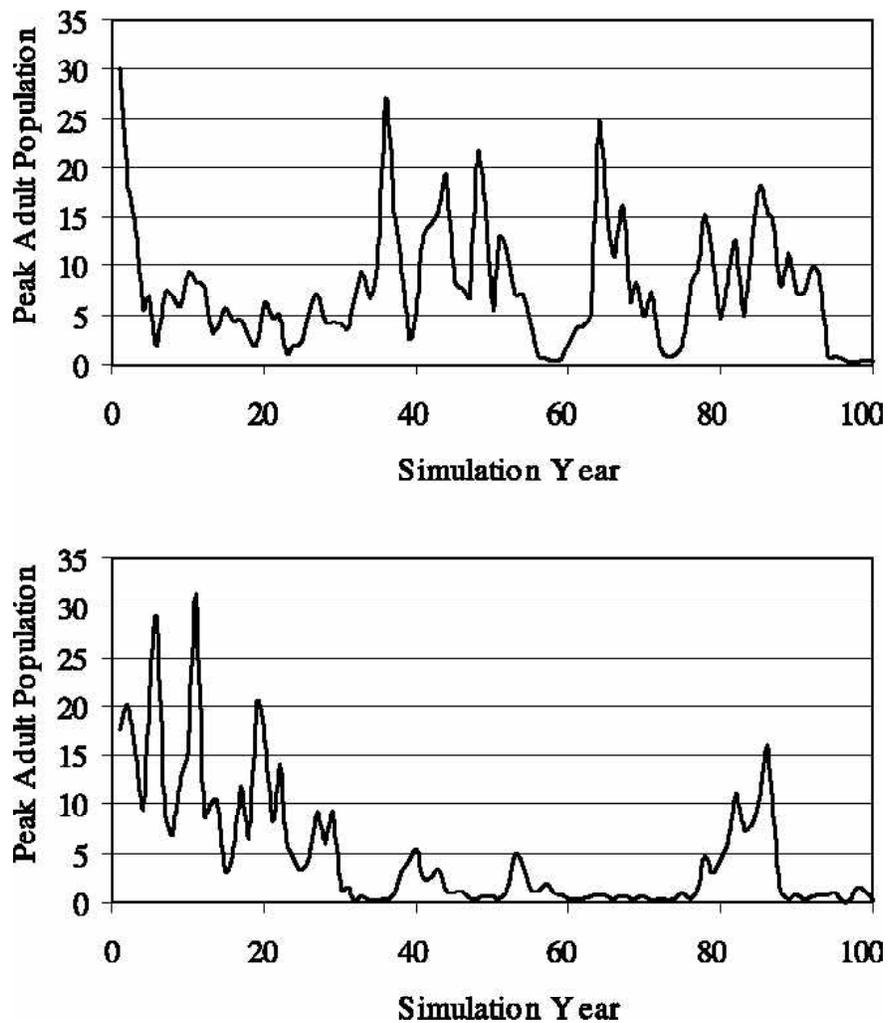


Figure 9. Annual time series of peak adult population (m^2) in corrected model in Ithaca (top) and Brookings (bottom) for a May 21 plant date and peak flower on August 29. Average peak adult population is 7.7 in Ithaca and 5.0 in Brookings.

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