Modeling the interaction of physiological time, seasonal weather patterns, and delayed mating on population dynamics of codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae)

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Abstract The effect of delaying female mating on population growth in codling moth (*Cydia pomonella* (L.)) was found to act on a physiological time (degree-day) basis and was predictable using a simple quadratic equation. When combined with previous work on degree-day based mortality, we were able to evaluate how the magnitude of population reduction and survival varied between sites, years, and generations at locations in California, Michigan, Pennsylvania and Washington states. In general, reductions in population growth associated with females mating 1–3 days after emergence were greater in warmer areas and during warmer times of the year. In any given year and location, the temperature profiles during peak flight were crucial in determining the population reductions, but over an 11-year period, the average seasonal temperature profile was more important. During the overwintering generation, conditions were relatively mild in all locations and only minor differences were observed in population growth rates between locations. Populations experiencing 1–3 days delay in female mating were reduced 8, 19 and 32 % compared to populations experiencing no delay, respectively. During the first summer generation, population reductions doubled compared to those seen in the overwintering generation. During the second summer flight, reductions in population growth rate at the three cooler locations decreased, while they increased in the warmer California location. Overall, the results show delayed mating can help understand how population growth is related to environmental conditions experienced naturally by insect populations and will help guide studies of the mechanisms of mating disruption, a technique used for pest suppression in agricultural and forest systems.

Introduction

The development of mating disruption as a method of insect control has stimulated interest in how mating disruption affects the population biology of the target pest. Initial inquiries were primarily focused on behavioral mechanisms by which mating would be prevented (Bartell 1982; Carde and Minks 1995), but field studies with various insects have shown that the percentage of mated females captured in mating disruption areas may be relatively high (although suppressed) compared to control (non-mating disruption) areas and still result in good damage suppression (Agnello et al. 1996; Knight 1996, 2000, 2007; Knight et al. 1996; Lawson et al. 1996; Fadamiro et al. 1999). This apparent contradiction meant that a focus on the possible mechanisms of mating disruption needed to include other mechanisms that might reduce population growth even though mating was not prevented. Barclay and Judd (1995) provided a theoretical overview of a wide range of potential mechanisms operating under mating disruption scenarios that might be contributing to population suppression. One of the outcomes of the Barclay and Judd (1995) article was the suggestion that female mating may not be prevented, but merely delayed because it is harder to locate a mate under mating disruption. The consequences to population growth for delayed mating would likely be less than outright

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prevention of mating, but might still have important consequences (Barclay and Judd 1995). These conclusions are readily supported by population biology, which maintains that the age at the start of reproduction is one of the most important factors governing population growth rates (Lewontin 1965; Carey 1993).

Since the article of Barclay and Judd (1995), there have been a large numbers of studies (see references in Jones and Aihara-Sasaki 2001) with a wide range of insects (primarily lepidopteran species) showing the population consequences of delaying mating. These studies show that as the delay in mating increases, the population growth rate declines, often because of a combination of sterility, reduced mating fitness, reduced fecundity, and/or age related factors unrelated to sterility (e.g., shorter oviposition period after mating) (Jones and Aihara-Sasaki 2001). The use of life tables has been a particularly powerful tool in investigating these effects, in part because life table statistics allow the use of relatively simple Leslie matrix models to evaluate long-term effects of different length delays and sensitivity analysis to evaluate the importance of different factors (Carey 1993, 2001; Caswell 2001; Jones and Aihara-Sasaki 2001; Jones et al. 2008a).

Despite the large body of work showing the importance of delaying mating for certain time periods on population growth, one of the key questions that has not yet been directly addressed is whether the effects act on a calendar date basis or on a physiological time [heat-unit or degree-day (DD)] basis. All of the studies to date that have quantified the effects of delayed mating have been performed under a given set of temperature conditions and a constant calendar time basis (e.g., delays of 0, 2, 4 or 6 days at 23 °C). While insect development and mortality processes are known to act on a physiological time basis, we are not aware of any studies that directly address whether delay of mating acts on a calendar or physiological time basis. The lack of this information is a significant impediment to developing population models that address not only delay of mating under mating disruption, but also our ability to understand the effect of abiotic factors (e.g., heat, wind or rain) that may delay mating naturally.

Insect mating behavior further complicates the question of mating delay. For many insects, mating can be considered to act as a gated rhythm that occurs only during a restricted part of the day; if mating does not occur during that period, a female must wait for the next day when the mating period begins again. For our target insect, the codling moth, Cydia pomonella (L.) (Lepidoptera: Tortricidae), the mating period has been reported to start roughly 3 h before dusk and end roughly 2 h after dusk (Wong et al. 1971; Batiste et al. 1973). Thus, a female codling moth that has not mated during the 5-h window, must survive another day before a second chance at mating

can occur. Therefore, if mating disruption acts strictly on a physiological time basis, the magnitude of the delay becomes a function of how many days female mating is delayed and the heat units that accumulate during that period. This means that the effect of delayed mating is not constant over calendar time and varies with season and ambient weather conditions.

In this paper, we integrate previous codling moth research including life table studies on the effect of delayed mating, heat-driven mortality in the field, phenology models that determine seasonal trends in emergence, and new studies to determine if delay of mating indeed operates on a physiological time or calendar date basis. This information is then used to construct a model to evaluate the importance of delayed mating based on weather data from four different locations where codling moth is a severe pest of apple, pear, or walnut over the period 2000–2010. Our focus in this paper is not the actual causes of delayed mating (e.g., mating disruption or natural abiotic factors), but rather the consequences of them and how those consequences may affect our understanding of population dynamics in situations where delays of mating may occur.

Materials and methods

Comparison of delays on calendar versus physiological time basis

Codling moths used in the experiments were reared on an artificial diet and obtained from the USDA-ARS Yakima Agricultural Research Laboratory in Wapato, WA; the insects were of the non-diapausing strain. Moths were shipped to Washington State University's Tree Fruit Research and Extension Center (WSU-TFREC) in Wenatchee, WA as last instar larvae and pupae in cardboard bands. In the laboratory, the pupae were removed from the bands, sorted by sex, and placed in cages (3 L) for emergence in a temperature cabinet (22 °C, RH ≈ 75 %) with a 16:8 h (L:D) photoperiod. Codling moth has a lower developmental threshold of 10 °C (Riedl et al. 1976; Howell and Neven 2000), so that by changing the temperature upon emergence, we could differentially "age" females by holding them at different temperatures for various periods of time. In this experiment, newly eclosed females were held for either 10 days at 15 °C (5° DD per day × 10 days = 50 DD delay in mating) or 2 days at 30 °C (20 DD per day × 2 days = 40 DD). After aging, females were returned to the 22 °C temperature cabinet where they were paired with 1-day-old males. Reproductive rate was measured over the remainder of adult female life by monitoring daily egg production and hatch rates using the methods of Jones et al. (2008a). Methods were the same for control moths, except that females were paired and placed in

the 22 °C temperature regime on the day of emergence. In all cases, females were paired with 1-day-old males and followed until female death. All DD reported in the paper are degree-days Celsius.

Life table statistics were used to evaluate the reproductive rate for the three groups of moths. We specifically chose the aging techniques above to maximize the age differences between moths on a calendar date basis (8 day difference) and minimized their age on a DD scale (10 DD difference). Thus, if delay of mating operates on a calendar date basis, the prediction would be that the control moths paired on the day of emergence would have the highest reproductive rate, followed by a significantly lower reproductive rate for the moths held at 30 °C for 2 days before pairing. Moths aged 10 days at 15 °C would have an extremely low reproductive rate. However, if the delay in mating acts on a physiological time basis, the control moths would have the highest reproductive rate and the two groups of aged moths would have similar reproductive rates. Because of the 10 DD difference in physiological age, we expect that the moths held at 30 °C (40 DD delay) would have a slightly higher reproductive rate than those held at 15 °C (50 DD delay). Analysis of this section was done on a calendar date basis.

Model development

The model to evaluate the effects of delayed mating on the population growth rate of codling moth with respect to both seasonality and location was based on several previously published studies. These studies had developed a robust codling moth phenology model driven by heat unit accumulations with a lower threshold of 10 °C and upper horizontal threshold of 31 °C (Riedl et al. 1976; Welch et al. 1978; Jones et al. 2008b). The phenology model was modified to provide the daily-predicted moth emergence as a proportion of the total per generation, rather than to provide the proportion of moths present (both newly emerged and older ones that had not yet died). These emergence curves were then fit to Johnson SB distributions using EasyFit (http://www.mathwave.com/) (one equation per generation) for use in the model to predict the effects of seasonality and location on population growth. The Johnson SB probability generating function is defined as:

$$f(x) = \frac{\delta}{\lambda \times \sqrt{2\pi} \times z \times (1 - z)} \times \exp\left(-0.5 \times \left(\gamma + \delta \times \ln\left(\frac{z}{1-z}\right)\right)^2\right) \quad (1)$$

and $z = \frac{x - \xi}{\lambda}$ where γ and δ are shape parameters ($\delta > 0$), λ is a scale parameter and ξ is a location parameter (Table 1). The model to evaluate seasonality and location effects was run only for the first 3 generations (overwintering, the first

and second summer generations) of codling moth in all locations. California has enough heat units to complete another generation in the Arvin location before diapause induction, but the other three areas do not; we were primarily interested in comparisons between the first three generations. Extending the number of generations evaluated is also complicated by diapause requirements, which are triggered by photoperiod and vary between locations (Riedl and Croft 1978).

The second component of the population growth model required the daily mortality rate of newly emerged individuals that mated at different times after emergence. To determine adult codling moth mortality that occurred before mating, we used the equations of Jones and Wiman (2008) which quantify adult codling moth mortality in the field on a DD basis. To use those equations, we calculated the number of DD using a 10 °C lower threshold and no-upper threshold. These DD will be called DD_{mort} as opposed to DD_{dev} (DD for development) that use a 10 °C lower and a 31 °C upper horizontal threshold. We then used a Gompertz equation to estimate age-specific survival (l_x):

$$l_x = \exp\left(\frac{A_0}{G} \times \left(1 - \exp^{(G \times DD_{mort})}\right)\right) \quad (2)$$

In Eq. 2, A_0 is the initial mortality rate per DD, G is the death rate per DD_{mort}, and DD_{mort} is the physiological time since adult emergence. The values for A_0 and G were set to 0.0026 and 0.0448, respectively (Jones and Wiman 2008). All DD were estimated using maximum and minimum temperatures based on the single sine approximation (Baskerville and Emin 1969).

The third major component was the effect of the delay in mating on the intrinsic rate of population growth (r_m). For this portion of the model, we combined the life table studies of Jones et al. (2008a) and those done in the comparison of the calendar versus physiological time study discussed above. From the Jones et al. (2008a) study, the effect of delays of 0, 2, 4, and 6 days on r_m were converted to a DD scale (those tests were run at 22 °C, so 12 DD per day were accumulated giving delays of 0, 24, 48, and 72 DD). The data from this study comparing physiological and calendar date mating delays added data points for 0 (control), 40 and 50 DD delays. We used the field-estimated survival (l_x) each day from Eq. 2 and age-specific fecundity rates (m_x) values from the lab studies to calculate r_m values based on DD. As with the studies of Jones et al. (2008a), we assumed that l_x at the time of adult eclosion was 0.36; even if the actual l_x at eclosion differed from this value, it would not affect comparisons since all treatments had the same initial values. The r_m values obtained were plotted versus the delay on a DD scale and we used a second-degree polynomial regression (SAS Institute Inc 2010) to

Table 1 Coefficients used in the Johnson SB distribution probability generating function for adult emergence of codling moth used in the simulation and start and stopping times in degree-days (DD) for the different generations

Generation	γ	δ	λ	ξ	Start DD	End DD
Overwintering	1.0737	1.2394	577.2	69.0	68	552
First Summer	0.3968	1.4682	825.6	494.8	557	1152
Second Summer	0.0876	1.0923	746.9	1101.2	1157	1757

estimate the relationship using all the data points from this study and that of Jones et al. (2008a).

For each day of the season and each delay, we calculated the number of progeny produced (N_t) using the exponential growth equation:

$$N_t = N_0 \exp(r_m \times t) \tag{3}$$

where r_m was calculated using the second-degree polynomial discussed above and t is the generation time in DD. We were primarily interested in how the population growth would change between locations and generations, so the initial number of individuals (N_0) in the simulations were always set to 100 per generation (i.e., the effects of delayed mating did not accumulate between generations). The value of r_m each day for a given delay was calculated using the polynomial regression of r_m versus DD delay and weighted by the number of emerging moths as given by the Johnson SB distribution (Eq. 1; Table 1). The generational totals were summed for each delay, compared as a simple proportion of the no-delay control treatment, and presented as box plots over the 2000–2010 period for each generation within a location.

Model evaluation

We evaluated the effect of delayed mating using field temperatures from 2000 to 2010 at four locations representative of apple or walnut production areas in Washington, Michigan, Pennsylvania and California. These included: (1) WSU-TFREC in Wenatchee, WA (apple); (2) Arvin, California (CMIS station #125) which is one of the more southern walnut producing areas in California's Central Valley, (3) Michigan State University's Trevor Nichols Research Center in Fennville, MI (apple), and (4) the Penn State University Fruit Research Center in Biglerville, PA (apple).

Because codling moth emerges at different DD accumulations across its geographical range, the model needed to be synchronized using the historic data of the first moth emergence for each location (i.e., the first moth acts as a biofix for the phenology). To allow a single set of Johnson SB curves to be used at each location, we used the historic average DD accumulation for capture of the first moth to standardize all sites so that the first capture occurred at 96

DD, which is the average timing observed in Washington State (Jones et al. 2008b). For example, the historical average time of the first moth capture at the California location was 270 DD (SE 14.3) (W. Bentley, unpublished data), so for calculating emergence and generation time, we subtracted 174 DD (=270 − 96) from the California DD accumulations. The historical time of the first emergence for the Michigan and Pennsylvania sites averaged 129 (SE 4.6), and 147 (SE 8.1) DD, respectively.

We evaluated the results in two ways:

(1) The daily l_x values were graphed for each of the delays at each location/year and the phenology model outputs were overlaid to see how phenology aligned with heat-driven mortality. Summary statistics were calculated and displayed with weighted boxplots; the weighting function was the daily phenology model output.

Boxplots are a way to visually summarize a distribution and its variability. The upper and lower quartiles of the data delineate a box and the median (50 % data) is represented by a horizontal line in the box. The whiskers of the box extend $\pm 1.5 \times$ the interquartile range (75th percentile–25th percentile) from the upper and lower quartiles. Any data outside the whiskers is called an outside point and plotted.

(2) The daily reproductive rates were graphed for each of the delays at each location/year and the phenology model outputs were overlaid to show how phenology affected reproduction rates. Summary statistics were calculated and displayed with weighted boxplots; the weighting function was the daily phenology model output.

Results

Comparison of delays on calendar versus physiological time basis

The life table parameters clearly show that the control females that experienced no delay in mating had the highest net reproductive rate and r_m (Table 2). The differences between the two groups of aged moths was relatively minor, and followed the prediction that females aged at 30 °C (40

Table 2 Comparison of life table parameters for codling moth aged on a degree-day scale in three different ways before mating

Life table parameter	No delay controls	Delayed 2 days at 30 °C	Delayed 10 days at 15 °C
Mating delay (DD)	0	40	50
Net fertility rate	18.9	9.1	7.7
Fertile eggs/female/day	7.4	4.9	4.9
Net reproductive rate (R_0)	15.0	9.7	8.6
Population double time (days)	13.9	16.6	18.1
Intrinsic rate of growth (r_m)	0.0500	0.0418	0.0384
Mean generation time (days)	55.2	57.3	66.5

After aging, all experiments were run at a standard 22 °C. Life table parameters were calculated on a calendar date basis

DD) would have significantly lower population growth rate than the control moths and only a slightly higher growth rate than the moths aged at 15 °C (50 DD). The fact that the moths aged 10 days at 15 °C were even close to the net reproductive rate of the moths aged at 30 °C confirms that the delay in mating does not act on a calendar date basis.

Relationship between r_m and degree-day delay

The relationship between r_m and the mating delay in DD was well described by a quadratic polynomial regression ($F = 869.3$, $df = 2,6$, $P < 0.0001$, $R^2_{adj} = 0.997$) (Fig. 1). Examination of the equation showed that all coefficients were significant (intercept $= 0.004$, $P < 0.0001$; DD delay $= -1.065e-5$, $P = 0.0448$; [DD delay]$^2 = -5.829e-7$, $P = 0.0004$). The close fit of the regression and the results of the laboratory study above give strong evidence that delay of mating acts on a DD scale and that any delay greater than ≈ 74 DD resulted in no population growth.

General behavior of the model

The predicted effect of a delay on population growth is much larger than that attributed solely to increased mortality (Fig. 2). At any DD accumulation from 0 to 70 (spanning the range of DD delay observed over all sites and years for delays of 1–3 days), the model predicts that the population size drops much quicker than the survival curve until about 50 DD, when the rate of change of the survival curve increases more rapidly. The quicker drop of the population curve initially is not a surprise, because survival is used to calculate the intrinsic rate of growth of the population.

Model evaluation between generations and locations

The temperature profiles at each location drive both the average phenology of codling moth and the average effect
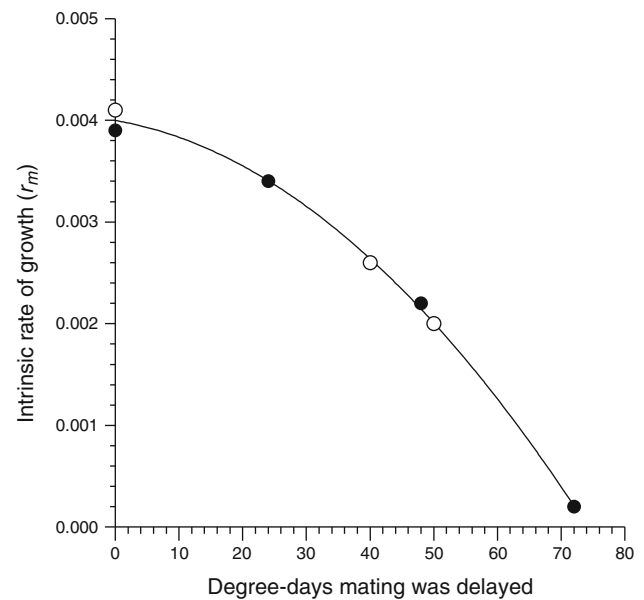

Fig. 1 The effect of delayed mating on the intrinsic rate of population growth (r_m). *Closed circles* are data from Jones et al. (2008a), *open circles* are data from this paper. All data are used in calculation of the regression line
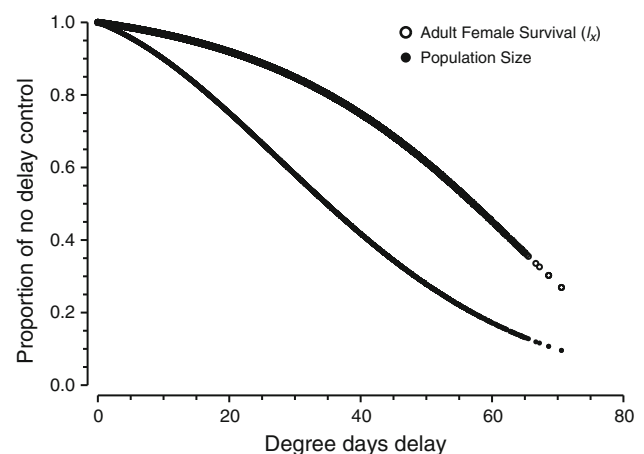

Fig. 2 Comparison of the effect of delayed mating on adult female survival (l_x) and on population growth compared to the no delay control population using the simulation model. *Curves* are drawn for the full range of delays experienced at all sites and years

on population growth for each generation. However, year-to-year variations in when high and low temperature periods occur affect the overall population dynamics in any given year at each location. For example, if a high or low temperature event occurs between generations (Fig. 3, points a and c) the effects on population dynamics are minimal because few individuals experience the delays. In contrast, the type and magnitude of the temperature events at peak emergence (Fig. 3, points b and d) is much more important because a greater part of the population

experiences the delays. Each location also has a different average seasonal temperature profile, which modulates the population growth profiles (Table 3). For example, daily DD accumulations for the California location increase throughout the season and just drop off by a few DD during the second summer generation flight (Fig. 4a). Daily DD accumulations at the other three locations showed more of inverted "V" or "U" shapes, with average daily DD accumulations in the overwintering and second summer generation flights always decreasing from a peak in the first summer generation flight (Fig. 4b–d).
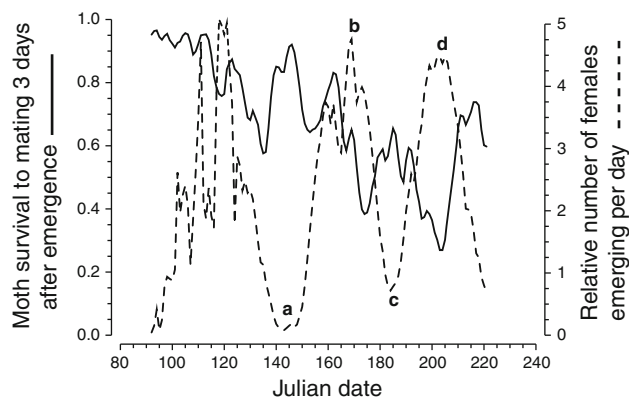

Fig. 3 Moth survival to time of mating if there was a 3-day-delay in mating throughout the season in 2006 at the Arvin, California site (*bold line*). Also included is the model estimate of the relative number of adult females emerging versus Julian date (*broken line*). Points "a" and "c" occur between flights and temperature profiles during that period are of minor importance to population dynamics. Points "b" and "d" occur near peak emergence and temperature profiles at that point have a much greater impact on population dynamics

Female survival between 2000 and 2010 showed little difference between locations when a 1-day mating delay occurred (Fig. 5a–c). As expected, the longer the delay, the greater the reduction in survival and the greater the variability. California consistently showed the greatest reductions in survival during the first and second summer generation flights. Michigan consistently had the greatest survival during the first and second summer generation flights, while the differences in survival between Pennsylvania and Washington were small and varied between the two generations.

Relative population sizes show that during the overwintering generation flights, there was essentially no significant difference in the relative population size between locations for each delay (Fig. 6a). Washington had a slightly cooler temperature profile than the other three locations at this point in time, which made relative population sizes less variable (i.e., the interquartile range is smaller). However, in all locations the progression from 1 to 3 days delay resulted in lower population size. During the first summer generation flight, the increasing temperature is especially evident in the greater effect of delayed mating from 1 to 3 days (Fig. 6b). The median reduction in population size is roughly twice that observed in the overwintering generation flight. By the second summer generation flight, the three northern locations had begun to cool dramatically, making the effect of the delay on population growth similar to that observed in the overwintering generation flight. However, at the California location, temperatures remained high, which made the population suppression for each days delay in mating significantly greater than that seen at the other locations (Fig. 6c).

Table 3 Differences in degree-day accumulations for delays of 1–3 days, average start and end date, length of generations of codling moth, and proportion of second summer generation completed in the period of 2000–2010 for the four different locations

Location	Generation[a]	Mean degree-days for delay of			Mean date		Generation length (days)	Prop. 2nd Summer gen. completed
		1 day[b]	2 days[b]	3 days[b]	Start	End		
California	1	8.2 ± 0.14	16.2 ± 0.28	24.0 ± 0.40	27 March	25 May	59	
California	2	15.1 ± 0.14	30.3 ± 0.27	45.5 ± 0.38	26 May	6 July	42	
California	3	17.8 ± 0.12	35.5 ± 0.23	53.1 ± 0.34	7 July	13 August	36	1.0
Michigan	1	9.4 ± 0.16	18.4 ± 0.31	27.3 ± 0.44	10 May	8 July	59	
Michigan	2	11.9 ± 0.13	23.6 ± 0.24	35.1 ± 0.33	9 July	31 August	53	
Michigan	3	7.6 ± 0.17	14.5 ± 0.33	20.9 ± 0.47	1 September	26 October[c]	55	0.61 ± 0.27
Pennsylvania	1	8.9 ± 0.17	17.4 ± 0.34	26.0 ± 0.49	23 April	22 June	60	
Pennsylvania	2	13.8 ± 0.13	27.5 ± 0.25	41.7 ± 0.35	23 June	6 August	44	
Pennsylvania	3	11.5 ± 0.15	22.6 ± 0.28	33.5 ± 0.40	7 August	24 October	60	1.0
Washington	1	7.7 ± 0.13	15.2 ± 0.24	22.5 ± 0.34	22 April	28 June	68	
Washington	2	14.5 ± 0.13	28.9 ± 0.25	43.3 ± 0.35	29 June	12 August	44	
Washington	3	9.4 ± 0.15	18.5 ± 0.30	27.2 ± 0.42	13 August	23 October	71	0.94 ± 0.06

[a] 1, overwintering generation; 2, first summer generation; 3, second summer generation

[b] Mean ± SE

[c] Third flight rarely completed

Fig. 4 Average daily degree-day accumulations at four locations for the period of 2000–2010. *Open circles* are the overwintering generation flights, *sold circles* are the first summer generation flights, and *open triangles* are the second summer generation flights. *Broken lines* separate the three flights (generations). **a** California. **b** Michigan. **c** Pennsylvania. **d** Washington
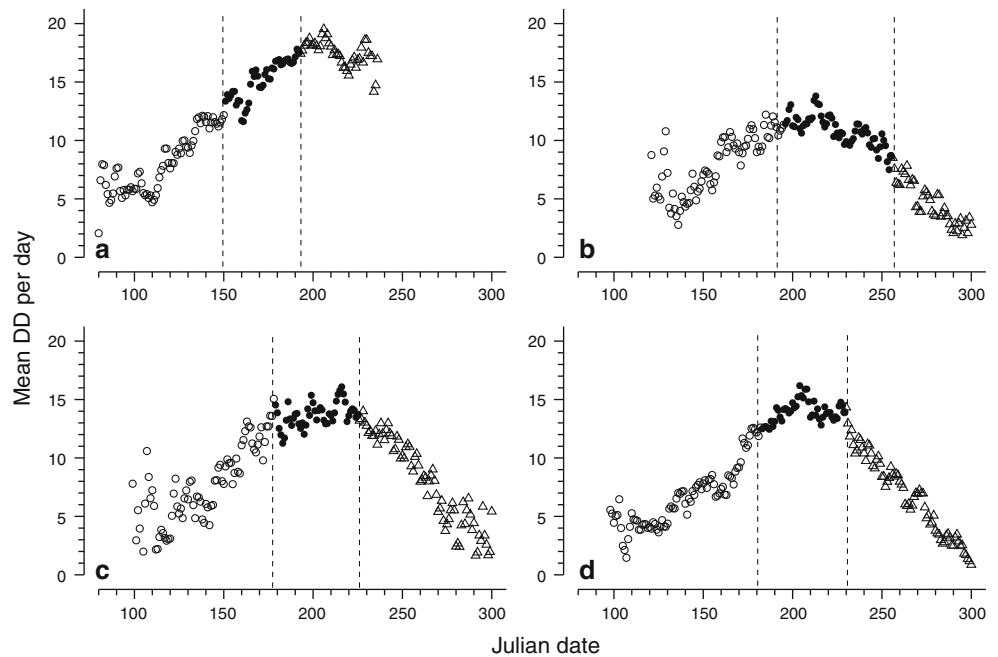
Discussion

Our model is directed towards understanding the effect of delays in mating on population growth irrespective of the reasons for those delays. Clearly, there are both abiotic (e.g., temperature, wind speed, rainfall) and biotic factors (e.g., Allee effects, asynchronous emergence, larval aggregation pheromones) that occur in natural situations (Robinet et al. 2007) or in managed agro-ecosystems that may increase or mitigate delays in mate finding. However, while inclusion of these factors might give a better overall understanding of how delays in mating occur, in the end, they would not improve our understanding of the consequences of delayed mating on population dynamics, only its causes.

Our data show that the effect of delayed mating on population growth is clearly driven by physiological time, similar to development and natural mortality rates. Moreover, if mating or flight patterns of the insect in question are gated rhythms of only a few hours duration each day, the delay can be quantified by simply looking at daily heat unit accumulations. For the codling moth, our data show that a delay of 3 days in the spring is needed to cause an average median reduction in population size of 32 % compared to the no delay control. During the warmest times of the year, average reductions in median population sizes of 32–51 and 52–76 % are possible for delays of 2 or 3 days, respectively.

The model also shows site-specific differences in the effect of delaying mating. These differences are a combination of the total amount of heat that accumulates over the season (determining how many generations occur) and the

points in the phenology of the insect where short-term high or low temperature periods occur. Evaluation of multiple years allows a better picture of how mating delays affect population growth for any particular location, but masks the effects possible within a year. Although not directly addressed in our study, how global climate change affects the importance of delayed mating (in general) will also be site-specific and investigators will need to evaluate not only the average magnitude of the change, but also the time of the season when the temperature profiles are modified. For example, warmer winters may have little effect on population dynamics (other than potentially earlier emergence) compared to warmer temperatures in the spring when delays on a DD scale may be markedly increased.

It is important to remember that the model assumes equal immature mortality between locations. This may or may not be true, especially for the California location where the host plant was different and the temperature profile was considerably different from that at the three more northern latitudes. In addition, at least at constant temperatures, survival through the different life stages is temperature dependent, with both low and high temperatures reducing survival (Pitcairn et al. 1991). However, this factor is likely of minimal importance in our analysis, because we are comparing population sizes of the various delays to the control (no delay) treatment at each location. Absolute population size would be affected by immature survival, but not the relative measures we used.

While our focus is on the effect of delayed mating and not the cause, our work may provide important insights for researchers examining the mechanisms by which mating
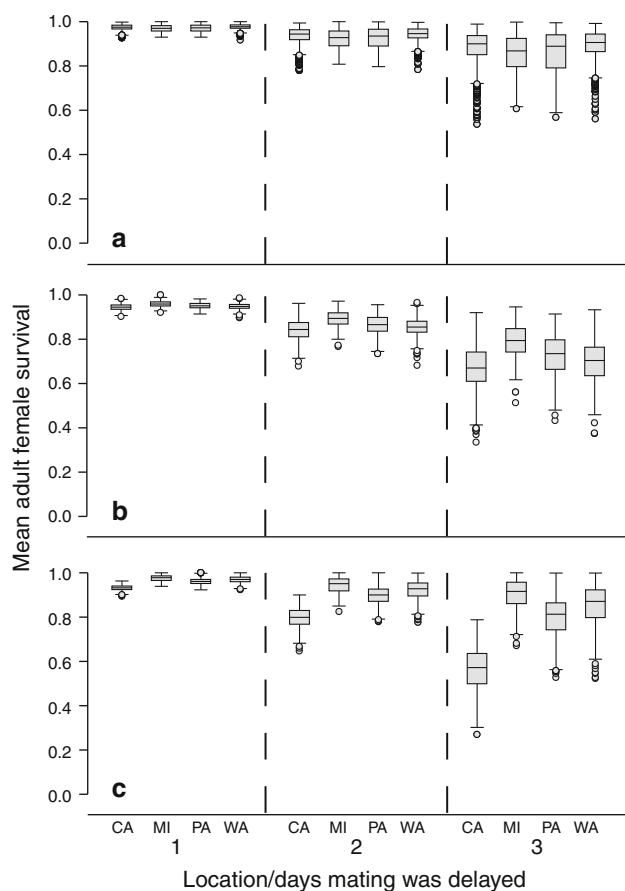
Fig. 5 Boxplots of the survival of adult females experiencing 1–3 days delay before mating for the period of 2000–2010 from the simulation model. *Broken lines* separate 1–3 days delay data. **a** Overwintering generation flight. **b** First Summer generation flight. **c** Second Summer generation flight. For locations, *CA* California, *MI* Michigan, *PA* Pennsylvania, *WA* Washington

Fig. 6 Boxplots of the proportion of the no delay control population size by generation flight, location, and the number of days delay before mating from the simulation model. Each generation started with 100 individuals, and no accumulation of effects occurs between generations. *Broken lines* separate 1–3 days delay data. **a** Overwintering generation flight. **b** First Summer generation flight. **c** Second Summer generation flight. For locations, *CA* California, *MI* Michigan, *PA* Pennsylvania, *WA* Washington

disruption suppresses pest populations. The time of the season, temperature profiles, and phenology are all critical factors in understanding variability between experiments and locations. For example, in warm areas like our California site, having even a relatively short calendar day delay in mating during the first and second summer generation flights can have a much greater impact than a longer delay during the overwintering generation flight or second summer generation flights in cooler areas like Michigan, Pennsylvania or Washington. This means that mating disruption in warmer areas or warmer times of the year can be less efficient and still provide reasonable suppression of codling moth. Researchers attempting to reconcile differences between crops such as walnuts (grown in warm areas) and apples (grown in colder areas), should first evaluate the differences in delay of mating that occur because of strictly climatic reasons before speculating that behavior, reproduction, or host-plant effects are critical factors in efficacy.
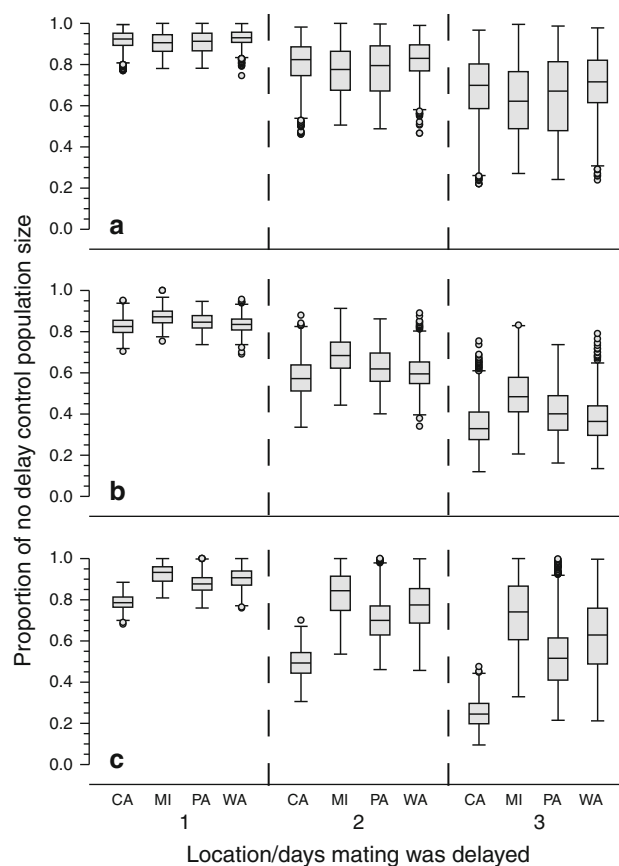
From a population growth perspective, the effect of mating disruption on codling moth can be completely described in terms of delayed mating. On one end of the spectrum, no delay in mating leads to optimal population growth. On the other extreme, when males are unable to find females, only sterile eggs are laid and population growth is zero. In between the two extremes, increasing delays result in an increasing inhibition of population growth fueled in part by increased mortality (Jones and Wiman 2008) as well as increased delay-related sterility and decreased egg production unrelated to sterility (Jones et al. 2008a). While complete suppression of mating has the greatest effect on population growth (only sterile eggs laid), our data show that once the delay exceeds ≈ 74 DD, there is no difference for all practical purposes to a complete lack of mating.

The effect of delayed mating may be less predictable or of less importance for some species, depending on species-specific longevity and reproductive capacity. For example,

obliquebanded leafroller, *Choristoneura rosaceana,* has a net reproductive rate nearly eight fold higher than codling moth and populations in the laboratory that experienced a 4 day delay in mating had a higher population growth rate than codling moth experiencing no delay (Jones et al. 2008a). The same principles used in this analysis still apply in terms of the effects on population growth, but from a practical perspective, a reasonable delay of mating (1–5 days) may not reduce population growth rates enough to allow mating disruption to be used as a management strategy. Synthesis of other studies on delayed mating using the physiological time model and using methods similar to those used in this study will help clarify the importance of delayed mating in studies on mating disruption as well as in natural situations.

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