

Projecting Insect Voltinism Under High and Low Greenhouse Gas Emission Conditions

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ABSTRACT We develop individual-based Monte Carlo methods to explore how climate change can alter insect voltinism under varying greenhouse gas emissions scenarios by using input distributions of diapause termination or spring emergence, development rate, and diapause initiation, linked to daily temperature and photoperiod. We show concurrence of these projections with a field dataset, and then explore changes in grape berry moth, *Paralobesia viteana* (Clemens), voltinism that may occur with climate projections developed from the average of three climate models using two different future emissions scenarios from the International Panel of Climate Change (IPCC). Based on historical climate data from 1960 to 2008, and projected downscaled climate data until 2099 under both high (A1fi) and low (B1) greenhouse gas emission scenarios, we used concepts of *P. viteana* biology to estimate distributions of individuals entering successive generations per year. Under the low emissions scenario, we observed an earlier emergence from diapause and a shift in mean voltinism from 2.8 to 3.1 generations per year, with a fraction of the population achieving a fourth generation. Under the high emissions scenario, up to 3.6 mean generations per year were projected by the end of this century, with a very small fraction of the population achieving a fifth generation. Changes in voltinism in this and other species in response to climate change likely will cause significant economic and ecological impacts, and the methods presented here can be readily adapted to other species for which the input distributions are reasonably approximated.

KEY WORDS greenhouse gas emissions, climate change, phenology, voltinism, grape berry moth

There is much interest in understanding the ecological effects of increasing concentrations of atmospheric greenhouse gases forcing climate change (Bale et al. 2002, Karl and Trenberth 2003, Meehl and Tebaldi 2004, Mills 2005, Curran et al. 2008), Zwiers and Hegerl 2008.) The Intergovernmental Panel on Climate Change (IPCC 2007a) projects increases in global mean surface temperatures of 1.1–6.4°C by the end of the 21st century if greenhouse gas emissions continue to increase at current rates. Such changes in climate will likely impact many ecosystem functions, especially many natural processes that are temperature dependent (Wing et al. 2005, Deutsch et al. 2008, Inouye 2008).

Insects are appropriate model candidates on which to study the effects of climate change. First, insects are poikilotherms and hence their internal temperature is highly dependent on ambient temperature. Consequently, insect development is driven primarily by temperature (Stinner et al. 1975, Logan et al. 1976, Pruess 1983, Tauber et al. 1986, Lowry and Lowry 1989, Wagner et al. 1984). Second, many insects have relatively short life spans, which is conducive to the

development of laboratory and field-based research designed to measure the impact of climate change. In multivoltine taxa, the number of generations per year under current and projected climatic regimes can be evaluated to quantify the influence of changing climates (Yamamura and Kiritani 1998, Van Asch et al. 2007, Post et al. 2008). However, many other factors, both biotic and abiotic, could also influence insect seasonality. For example, many insects diapause and often the main induction factor is photoperiod (Tauber et al. 1986, Denlinger 2002). Furthermore, the nonlinear interaction of temperature and photoperiod makes it challenging to investigate and understand changes in insect voltinism in response to climate change (Tobin et al. 2008). Although universal predictions of how climate change would influence insect phenology is not feasible, doing so for representative insect species could be valuable in efforts to understand the consequences of climate change in a general context.

Understanding key drivers of insect voltinism, such as development and diapause, are essential in efforts to quantify the consequences of climate change on insect seasonality (Logan et al. 2003). Such drivers are known for the grape berry moth, *Paralobesia viteana* (Clemens) (Lepidoptera: Tortricidae) (Nagarkatti et al. 2001, Tobin et al. 2001, 2002, 2003). *P. viteana* is native to North America and feeds on native wild and

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cultivated (not necessarily native) *Vitis* host spp., and can be an economically important pest in the latter (Riedl and Taschenberg 1984). It is also nonmigratory, and movement patterns are spatially limited; thus, life stages are not subjected to different temperature profiles, and projections of *P. viteana* at a given location are reasonable predictors of the effects of climate change. Adults emerge in spring from diapausing pupae, mate, and females oviposit on *Vitis* spp. flowers or fruit. Upon hatching, larvae burrow into the fruit, exiting to pupate in leaves or bark. Pupae emerge as adults that initiate subsequent generations. As day-length decreases after the summer solstice, there is a critical photoperiod independent of temperature that initiates diapause, and eggs deposited at these decreasing photoperiods will develop into diapausing pupae (Nagarkatti et al. 2001). Hence, as in many temperate insect species, voltinism is influenced by the degree-day accumulation before the arrival of photoperiodic conditions that initiate diapause. There are generally 2–3 generations per year along the grape production belt along Lake Erie (Tobin et al. 2003). Tobin et al. (2008) previously highlighted the consequence of interactions between temperature (subject to climate change) and photoperiod (not subject to climate change) in driving *P. viteana* voltinism. In this paper, we extend this work by examining the interaction of temperature and photoperiod based upon scenarios of the rate of greenhouse gas emissions and their effect on temperature (Hayhoe et al. 2007). We also present an individual-based Monte Carlo approach to quantify changes in voltinism and highlight not only generalized trends but the variability among individuals within a population, and provide open-source computer code to enable these methods to be extended to other species.

Materials and Methods

We developed our model based upon prior studies of *P. viteana* biology conducted at the Lake Erie Regional Grape Laboratory in North East, PA (42.2 °N, 79.9 °W) that describe development and diapause as functions of temperature and photoperiod (Nagarkatti et al. 2001, Tobin et al. 2001, 2002). Photoperiods for North East were obtained from the Naval Oceanography Portal (2008). Projected monthly temperature data for this location, estimated to the end of this century under both high (A1fi) and low (B1) greenhouse gas emissions scenarios of the IPCC Special Report on Emissions Scenario (Nakicenovic et al. 2000), are available from the Northeast Climate Impacts Assessment (2006). The A1fi scenario simulates climate under current economic development conditions without reducing greenhouse gas emissions, and the B1 scenario assumes significant global reductions in greenhouse gas emissions; these scenarios have been used previously to contrast climate-driven processes under different greenhouse-gas emissions scenarios (Hayhoe et al. 2007, Kunkel et al. 2008).

We obtained higher resolution downscaled daily weather data in the location of interest from 1960 to

2099 (M. F., personal communication) more detailed description of climate data downscaling techniques and applications is provided by Hewitson and Crane (1996). The data are the average of three general circulation models—the Geophysical Fluid Dynamics Laboratory model (GFDL), the Hadley Centre for Climate Prediction and Research model (HadCM3) and the National Center for Atmospheric Research Parallel Climate model (PCM)—each with a different sensitivity to changes in greenhouse gas amounts. Using these models with the A1fi and B1 emission scenarios, daily mean temperatures were derived.

Our population model is individual based and divided into three sub-models: diapause termination (Tobin et al. 2002), degree-day development (Tobin et al. 2001) and diapause induction (Nagarkatti et al. 2001). We focused our attention on modeling the progression of individuals among life stages independent of population density. These simulation processes are presented in Fig. 1 as a conceptual model.

Diapause Termination. Diapause termination in *P. viteana* is primarily driven by temperature, and initial and 50% adult emergence generally occurs at 148 and 210 DD accumulated after 1 January, respectively (base threshold = 8.4°C, Tobin et al. 2002). Because *P. viteana* overwinters as a pupa, the total degree-day requirement for adult emergence from diapausing pupae is different from that of the subsequent generations, which develop from egg to adult. Also, because the distribution of degree-day accumulation required for adults to emerge from diapausing pupae is often highly skewed, we used a negative binomial distribution with $k = 2$, which we estimated from field observations of emerging adults reported in Tobin et al. (2001), to simulate a distribution of the required degree-days at which emergence would occur. Because the minimum degree-day requirement is 148 instead of 0, which is typical of a binomial distribution, we shifted the distribution to the right, accordingly. The calendar day of emergence of each adult from a population of 10,000 diapausing pupae was then recorded. We defined this population of emerging adults as the first generation.

Development. After adult emergence, another 75 DD were added for female sexual maturation (Luciani 1987, Tobin et al. 2003). If we assume that females oviposit all eggs in a single day and only one offspring survives to the adult stage (e.g., the population size doesn't increase), we can treat the second generation offspring as another generation of its parent. For the second (and subsequent) generation(s), an average of 424 DD is required for development from egg to adult (Tobin et al. 2001). This developmental rate, however, also follows a negative binomial distribution, with a mean of 424 and $k = 2$, as determined from initial investigation of the field data (Tobin et al. 2001). We shifted this negative binomial distribution to the right by 250 because the minimum degree-day requirement for egg-to-adult development is 250 (Tobin et al. 2001). Each first generation adult was advanced independently with respect to the distribution of egg-to-adult development. This yielded the required cal-

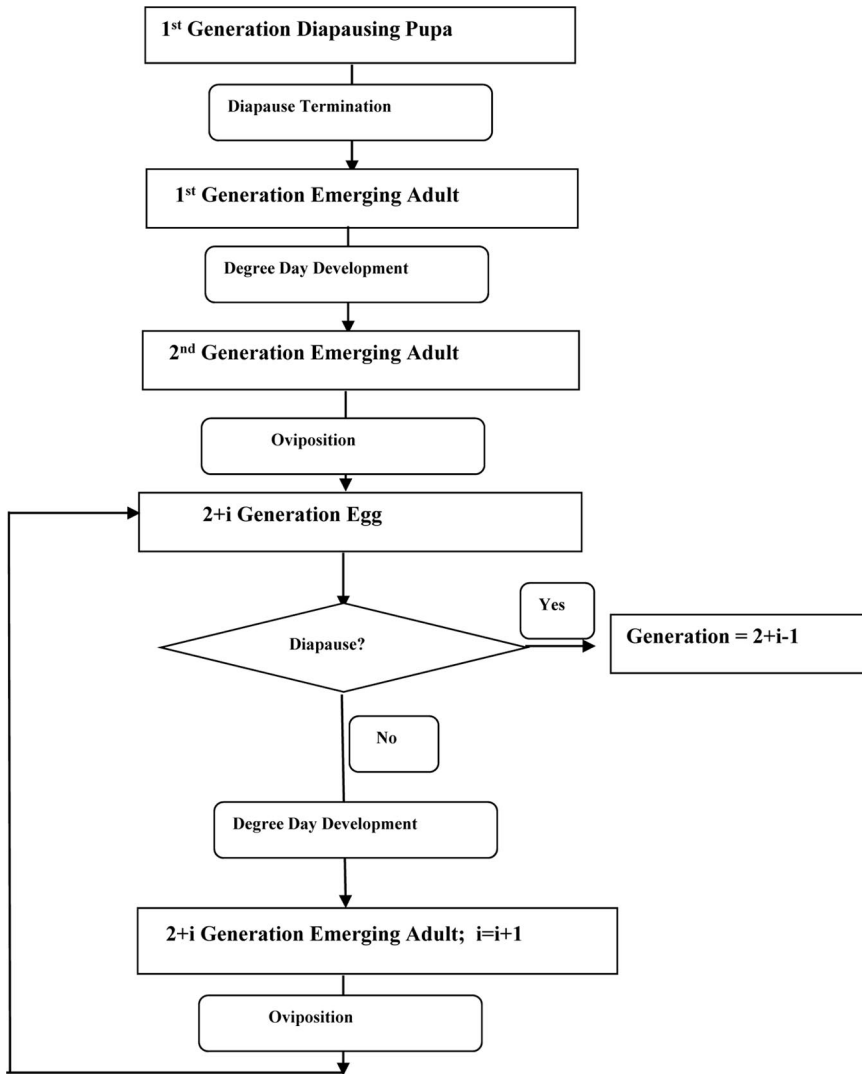


Fig. 1. Conceptual model for a single simulation run to collect number of generations per year, initialized by a diapausing overwintering life stage.

endar days for the development of the population of second generation adults.

Diapause Induction. The egg is the sensitive stage for diapause induction, and depending on the photoperiod at which an egg is laid, it will either eventually develop into an adult or into a diapausing pupa (Nagarkatti et al. 2001). In field studies, eggs laid before 25 June at the latitude of North East, PA never entered diapause, and after 11 August all eggs entered diapause (Nagarkatti et al. 2001). The probability of entering diapause, Pr , is thus a function of the change in photoperiod (in hours) between a given date and its precedent date after the summer solstice, Pc , when the egg is laid,

$$Pr = 100(1 - e^{-3.957Pc}). [1]$$

For any given individual, we used a uniform distribution to run a Monte Carlo simulation to determine

whether the individual of the second generation or later enters diapause. For instance, if the probability (Pr) of entering diapause is 0.7, we chose a random number generated from a uniform distribution [0,1]. If that random number was smaller than 0.7, then the individual egg developed into a diapausing pupa; otherwise, that egg matured into an adult. In the latter case, an additional 424 DD (determined from the development-rate distribution described above) would be accumulated by that individual to reach the adult stage, and another 75 DD would be accumulated to allow for oviposition by that adult. This iterative process was continued until all individuals were either in diapause or dead (i.e., degree-day accumulation was insufficient to complete the life cycle to an ovipositing adult).

Field Validation. Independent of these modeling efforts and the published literature, we conducted a

field study to determine the distribution of adult *P. viteana* emergence dates at North East, PA, in 2007. By using a combination of malaise traps and light traps, we monitored female *P. viteana* at four locations in the area of North East, PA. Unlike sex pheromone trap-catch data of male moths, which is useful to determine first generation emergence (Tobin et al. 2003) but not subsequent generations (M.C.S., unpublished data), female trap catch data provided us with discrete generational peaks that could be compared with the results from our simulations.

Simulation Models and Analyses. We simulated a population of 10,000 individuals, initialized as overwintering diapausing pupae, which progressed through diapause termination, development, and diapause initiation (Fig. 1). We first tested whether the negative binomial distribution was appropriate to simulate the degree-day requirement by conducting a two-sided Kolmogorov–Smirnov test. To model the influence of climate on the voltinism of this population, we determined two outcomes for each individual: 1) the number of generations each individual and its progeny could complete until it either entered diapause or died, and 2) the calendar date of adult emergence for each generation it experienced. Each individual could only complete one generation and have exactly one offspring, regardless of regulation factors such as predation and disease. Hence, each offspring represents a parent individual in the future generation, and we tracked the outcome for that individual. We quantified the number of generations from each iteration, and then used 10,000 iterations to calculate the distribution of the number of generations per year. In each generation, we also determined the distribution of emergence dates and the number of completed generations for the field-collected data from 2007, and two projected emission scenarios extending to the end of the century. We also compared the predicted and observed distribution of emergence dates using a two-sided Kolmogorov–Smirnov test for that year. The simulation code, presented in the Appendix, was written in MATLAB 2007 (The MathWorks Inc., Natick, MA). We summarized these outcomes as time-series plots, graphing the mean number of completed generations, and the mean calendar day of adult emergence extending to the end of this century, under the low and high emission scenarios developed from the average of GFDL, HadCM3, and PCM climate models.

We used linear regression, using the mean number of generations as a dependent variable and year as the independent variable, to test whether there was a significant increasing trend of mean generations per year under the historical and low emission condition projections. For the projected high emission condition, after initial scrutiny, we discovered a significant nonlinear trend; thus, we used nonlinear regression by fitting a Gompertz function because a Gompertz curve has asymptotic properties that are more realistic than other unrestricted nonlinear functions (Laird 1964).

To explore the seasonal dynamics of different generations under our climate change scenarios, we used the default kernel estimation function in R to estimate

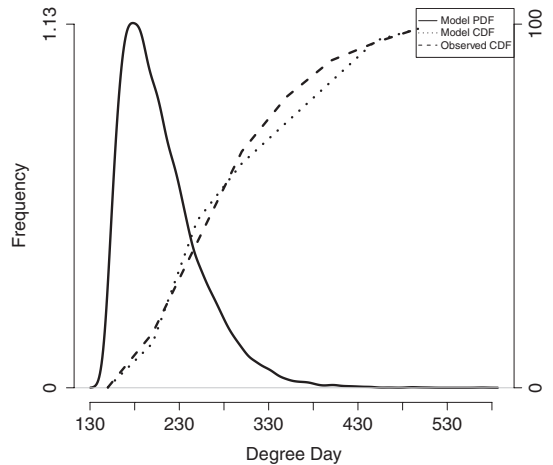


Fig. 2. Degree Day requirement of first generation emergence of adult grape berry moth from overwintering diapausing pupae. PDF is the density function, and CDF the cumulative density function. For both functions, modeled values are from Tobin et al. 2002, and observation are from field data collected in 2002.

the kernel density of each generation in 2007 (from the field data), and in the low and high conditions in 2099. These estimated kernel functions express the proportion of the population that is present for every date that each generation completes its life history. The area under the curve for each generation sums to one.

Under both the low and high emission scenarios, we investigated the shift in emergence date for all four generations throughout the simulation period, from 2009 to 2099. For each generation in both scenarios, we used linear regression of emergence date by year to test if there was a significant trend. Furthermore, we used Analysis of Covariance to test for differences in the emergence date over year (as a covariate), using the different emissions conditions (low and high emission) as a categorical main effect. All statistical analyses were conducted in R 2.10 (R Core Development Team 2010).

Results

The projected probability density function (PDF), projected cumulative density function (CDF), and observed CDF (Tobin et al. 2003) of adult emergence from overwintering, diapausing pupae are shown in Fig. 2 for 2001. The simulated distribution had predicted mean, minimum, and maximum degree-days of 210, 148, and 530, respectively, which coincides well with the observed data (mean, minimum, and maximum degree-days of 210, 148, and 512, respectively Tobin et al. 2003). We also observed congruence between model predictions and empirical observations in the emergence profile by conducting a two sided Kolmogorov–Smirnov test of the first generation (Fig. 2). The results show no significant difference between predicted and observed distributions ($D = 0.05$, $P =$

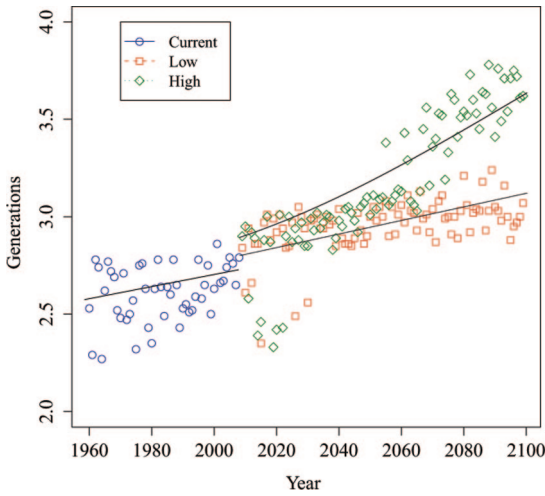


Fig. 3. Historical and projected number of mean generations of grape berry moth in North East, PA, under low and high emission conditions (B1 and A1fi emission conditions, respectively) described by the Intergovernmental Panel on Climate Change (IPCC 2007b). (Online figure in color.)

0.22), suggesting that the negative binomial distribution was appropriate in our efforts to simulate degree-day requirements for diapause termination and emergence of the first generation, which were then progressed through the development rate and diapauses initiation subroutines.

Using this modeling framework (Fig. 1), the estimated number of mean generations increased during the recent historical past (from 1960 to 2008), and is projected to continue to increase throughout the century in both greenhouse gas emission scenarios (Fig. 3). From 1960–2008, there was a significant increase in the number of generations ($F = 5.32$; $df = 1, 47$; $P < 0.05$). In both the low ($F = 29.49$; $df = 1, 89$; $P < 0.001$) and high ($F = 32.57$; $df = 1, 89$; $P < 0.001$) emission conditions, the number of generations was projected to increase (Fig. 3). To iterate, the projected number of generations in a specific year is the mean based upon 10,000 individual simulations.

The seasonal dynamics of different generations under different climate change scenarios can be illustrated by the distribution of adult emergence for each generation. The comparison between the simulated density function of emergence date for each generation in 2007 and observations from the field in 2007 is presented in Fig. 4 (top panel). Note that the amplitude of the first generation does not imply that its population size is larger than other generations; rather, the curve is a density function, capturing the total area under the curve such that the area sums to one for each generation. The emergence timespan of the first generation is more narrowly distributed than later generations, which leads to a higher amplitude. The observation curve is scaled so that the maximum number of observations in each generation is the same as the maximum value of the projected density func-

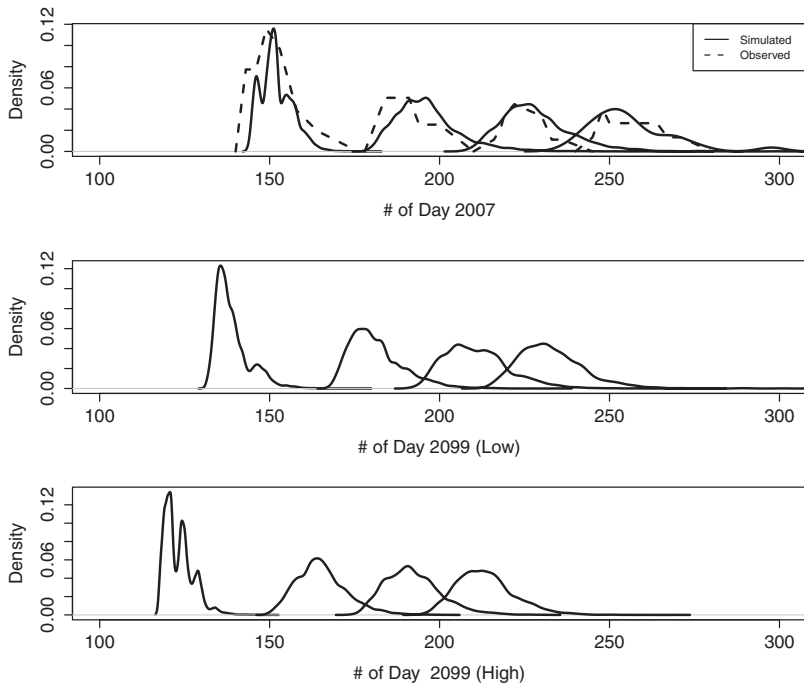


Fig. 4. Density functions expressing the emergence date for all generations of grape berry moth in 2007 (top panel, for observed data collected from malaise traps, and for simulated data), and for 2099 under low (middle panel) and high (lower panel) emission conditions (B1 and A1fi emission conditions, respectively) described by the Intergovernmental Panel on Climate Change (IPCC 2007b).

tion in that generation. Also, note that these curves reflect the distribution, but not the number, of individuals contributing to each generation. For example, in 2007, there were 13, 25, 38, and 11 individuals measured in the field for generations 1, 2, 3, and 4, respectively. The higher amplitude and shorter range associated with the first generation reflects the more discrete timing over which the first generation presents itself, in contrast to the wider ranges that result in overlapping generations in subsequent generations. We also ran a two sided Kolmogorov–Smirnov test and found no significant differences between predicted and observed distributions of emergence dates in all four generations ($D = 0.38, 0.87, 0.49$, and 0.21 , and $P = 0.35, 0.08, 0.19$, and 0.56 , for generations 1 through 4, respectively). From these comparisons, we verified that our modeling predictions almost match the observed field data; generally with a deviation of ± 3 d (Fig. 4, top panel). The exception was that our projected emergence date for the second generation was ≈ 5 d later than the observed date.

The estimated density functions of emergence date for each generation in 2099 under both low and high emission scenarios also are presented in Fig. 4 (middle and bottom panels). By the end of the century and under the low emission scenario, the initial emergence dates of the first two generations have advanced ≈ 15 – 20 d relative to 2007. For example, in the first and second generation, the timing of their respective initial emergence in 2007 is approximately the time at which 50% emergence is predicted to occur by 2099, although the third and fourth generations are predicted to be advanced ≈ 20 – 30 d relative to the 2007 data under the low emission scenario.

Under the high emission scenario, this tendency for advanced emergence is much more pronounced. All four generations advanced almost 30 d compared with 2007, and under this scenario, adult emergence from overwintering pupae is projected to be almost completed before observed emergence from 2007 would have begun. Moreover, $\approx 30\%$ of the second generation would be completed before a second generation in 2007 would have begun. This advance of a full generation follows throughout the time series, so by the time a rare fourth generation conceivably could have occurred in 2007, the model not only predicted four full generations in 2099, but also sufficient time for a partial fifth generation. We suggest this advance is because of a combination of earlier first generation emergence and faster developmental times in subsequent generations under climate warming.

The projected mean emergence dates from 2009 to 2099 under both emission scenarios are presented in Figs. 5 and 6. Under both the low and high emissions scenario, a very significant ($P < 0.001$) and negative trend toward earlier emergence dates was observed in all four generations as time progressed through the 21st century (Table 1). The slope estimates express the rate of decrease in number of days needed to complete each generation, and range from -0.120 to -0.278 under low emission conditions, and -0.316 to -0.548 in the high emission conditions. In both

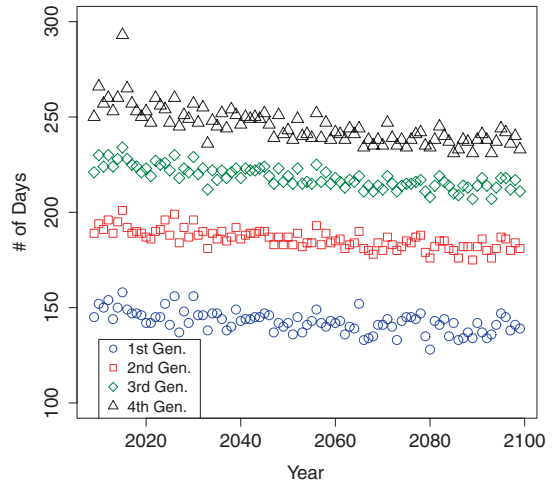


Fig. 5. Projected mean emergence date for all generations of grape berry moth under low (B1) emission conditions described by the Intergovernmental Panel on Climate Change (IPCC 2007b). (Online figure in color.)

emissions scenarios, there is a trend toward a faster decline (i.e., steeper negative slopes) as generations increase. Also, there is a consistent trend toward a more predictive relationship (a higher R^2) as generations increase within each emission condition (Table 1). Relationships of emergence date with year were consistently more predictive from simulations conducted under the high-emission condition (R^2 of 0.74 – 0.91) than the low-emission condition (R^2 of 0.31 – 0.58) (Table 1). When comparing the effect of emissions conditions given the time-dependent decrease for each generation using an analysis of covariance (ANCOVA), both the categorical variable (emission conditions) and covariate (year) had a highly significant influence ($P < 0.001$) on emergence dates (Table 2).

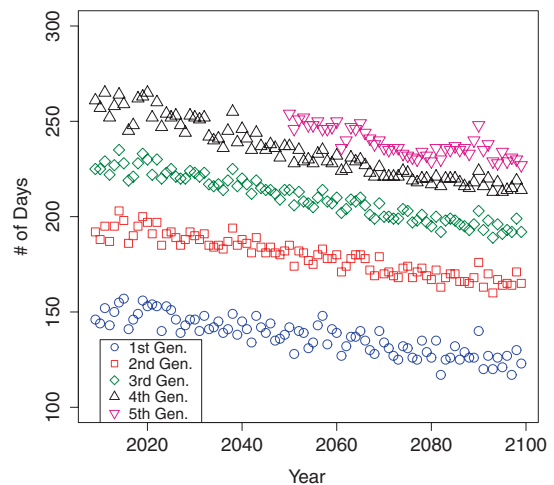


Fig. 6. Projected mean emergence date for all generations of grape berry moth under high (A1fi) emission conditions described by the Intergovernmental Panel on Climate Change (IPCC 2007b). (Online figure in color.)

Table 1. Regression of mean emergence dates (y) on years (x) under low (B1) and high (A1f) emission conditions

Emission condition	Generation	a	b	R^2	F	p
Low	1	-0.120	390	0.31	41	<0.001
	2	-0.137	468	0.50	91	<0.001
	3	-0.166	560	0.60	131	<0.001
	4	-0.278	817	0.58	123	<0.001
High	1	-0.316	786	0.74	247	<0.001
	2	-0.361	920	0.86	557	<0.001
	3	-0.426	560	0.91	907	<0.001
	4	-0.548	817	0.91	851	<0.001

The regression has the form y (emergence date) = ax (year) + b .

As noted by the density kernels (Fig. 4), there is an opportunity for a fifth generation to develop under the high emission scenario by the end of the century. In our summarization of mean emergence dates through time, we saw a very small proportion (≈ 50 out of 10,000 individuals) of the population entering a fifth generation under the high emission conditions, beginning in 2050 (Fig. 6).

Discussion

There is a need to estimate the influence of climate change on insect populations to provide guidance in policy decisions, and to enable adaptations in agricultural practices and public health efforts. Climate models under varying emissions scenarios are becoming increasingly available and statistically downscaled, both temporally and spatially, enabling abiotic drivers (temperature and photoperiod) of insect phenology models to connect to projections of climate change. Among the variables that define climate (i.e., temperature, precipitation, and wind), temperature is often the more tractable to predict as advances in statistical downscaling enable more reasonable predictions of local daily temperatures (Marshall et al. 2007), although photoperiod remains effectively constant. Thus, abiotic drivers of insect voltinism can be estimated. The degree-day requirements for spring emergence and in-season development have been estimated for many insect species (Taylor 1981, Nietschke et al. 2007); however, methods to connect these degree-day based insect phenology models with models of climate and climate projections still are needed. Here, we provide an individual-based approach to explore how climate change can alter insect voltinism under varying emissions scenarios by using input distributions of diapause termination or spring emer-

Table 2. Influence of low or high emission condition (modeled as a categorical variable) and year (modeled as a covariate) on mean emergence dates

Generation	R^2	F	p (emission condition)	p (year)
1	0.667	119	<0.001	<0.001
2	0.819	269	<0.001	<0.001
3	0.877	421	<0.001	<0.001
4	0.841	312	<0.001	<0.001

gence, development rate, and diapause initiation, linked to daily temperature and photoperiod. These individual-based methods enable projection of both means and distributions of emergence dates. We showed concurrence of these projections with a field dataset, and explored projections in our model system.

Our model system assumes that development of individuals is driven solely by air temperature, and diapause solely by photoperiod by using a population initialized at 10,000 individuals, which can only be reduced because of individuals entering diapause or because of mortality when individuals fail to complete development to a diapause-capable stage. We assumed no immigration, emigration, or variation among life stages in how they are exposed to air temperature. These simplifying assumptions enabled us to develop a modeling framework for examining the influence of future climates on voltinism at a single spatial location. Future work should consider climatic influences on populations over wider spatial scales, incorporating variation in the drivers of insect seasonality such as the effects of host quality (Hunter and McNeil 1997), and geographic clines in diapause initiation probabilities (Ruberson et al. 2001).

New York, Michigan, and Pennsylvania are respectively the second, fourth, and fifth largest grape producing states in the United States, and the vast majority of the grapes in these states are grown along the shores of Lake Michigan, Lake Erie, and in the Finger Lakes region of New York. All of these grape growing regions are close in latitude to North East, PA, from where the field study was based. In recent years, late season infestations of *P. viteana* have surprised many growers in this area, resulting in an increased amount of fruit being rejected for consumption because of insect damage (M.C.S., unpublished data). These late season infestations have caused considerable consternation to both growers and the industry. The timing of insecticide sprays against *P. viteana* populations have remained unchanged since 1991 with the introduction of the Grape Berry Moth Risk Assessment Program (Martinson et al. 1991). For a high risk vineyard, this protocol calls for an insecticide application at 10-d postbloom (targeting first generation *P. viteana*), early August (targeting the second generation), and if necessary, late August (targeting the third generation). Although the recommended first spray is tied to bloom time, which in turn, is driven by temperature, the timing of subsequent treatments is currently based solely on calendar date irrespective of temperature. During a growing season with average temperatures, these management guidelines could work fairly well, but are inadequate when temperatures do not follow an "average" year.

The reality of climate change will result in a need to adjust overall management guidelines for many insect species, including *P. viteana*, as well as dynamic strategies within the growing season to account for developmental and climatic variability. Recent failures in *P. viteana* management programs suggest that this shift in voltinism could already be happening. The economic damages associated with future additional generations of insect pests of agriculture, forestry, animal health,

and other sectors are likely to be severe (Walther et al. 2002, Kiritani 2006, Reisen et al. 2006, Kilpatrick et al. 2008, Lafferty 2009). We note that in *P. viteana*, the inherent lag associated with climate suggests that we will see increasing numbers of individuals reaching a third generation in North East, PA, regardless of policy or other factors that might influence emissions, until approximately mid-century (Fig. 3). It is not unreasonable to assume similar shifts in voltinism in other systems. After 2050, however, there is likely to be a dramatic influence of emission scenarios on *P. viteana* voltinism, particularly under the high emission scenario. It is important to note that we are defining the "high" emission scenario as a continuation of the status quo in emission rates, which is fossil-fuel intensive and is the highest future emission trajectory considered by the IPCC (Nakicenovic et al. 2000). However, recent observations show global emissions have been higher than this "high" emission scenario since 2004 (Canadell et al. 2007, Raupach et al. 2007).

In addition to the mean temperature, daily temperature variability also could significantly influence insect life history. Past work has demonstrated that changes in the range of daily temperatures can affect the longevity, mortality, and other life history variables in mosquitoes, which could in turn affect mosquito-borne disease dynamics (Paaijmans 2009, 2010). Because increasing climate variability is an important aspect of global climate change (IPCC 2007b), future studies also should focus on the influence of climate variability on insect voltinism in this and other systems.

Increasing levels of greenhouse gases likely will result in increases in annual global average temperature. This increase in turn will affect many aspects of ecosystem function, and will alter the dynamics and distribution of individual species and the communities in which they interact (IPCC 2007a,b). Here, we focused our attention to two emission scenarios: A1f and B1. Although insect voltinism is strongly determined by temperature and thus also would be affected by increasing temperatures, other factors such as photoperiod, which is not influenced by global climate change, also play an important role in insect seasonality. We show here how the nonlinear interaction between temperature and photoperiod is critical in understanding the link between climate change and voltinism. We also provide projected patterns of voltinism for a representative multivoltine insect species under these two climate change scenarios. Moreover, we also propose a conceptual framework, through the incorporation of diapause termination, degree-day development, and diapause induction for addressing climate change and voltinism in other insect systems. The conceptual framework, and the source code provided in the Appendix, could be readily modified for use in other systems.

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References Cited

- Bale, J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. M. Bezemer, V. K. Brown, J. Butterfield, A. Buse, J. C. Coulson, J. Farrar, et al. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Glob. Change Biol.* 8: 1–16.
- Canadell, J. G., C. Le Quéré, M. R. Raupach, C. B. Field, E. T. Buitenhuis, P. Ciais, T. J. Conway, N. P. Gillett, R. A. Houghton, and G. Marland. 2007. Contributions to accelerating atmospheric CO₂ growth from economic activity, carbon intensity, and efficiency of natural sinks. *Proc. Natl. Acad. Sci. U.S.A.* 104: 18866–18870.
- Curran, E. D., P. Wilf, S. L. Wing, C. C. Labandeira, E. C. Lovelock, and D. L. Royer. 2008. Sharply increased insect herbivory during the Paleocene-Eocene Thermal Maximum. *Proc. Natl. Acad. Sci. U.S.A.* 105: 1960–1964.
- Denlinger, D. L. 2002. Regulation of diapause. *Annu. Rev. Entomol.* 47: 93–122.
- Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haark, and P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl. Acad. Sci. U.S.A.* 105: 6668–6672.
- Hayhoe, K., C. P. Wake, T. G. Huntington, L. Luo, M. Schwartz, J. Sheffield, E. Wood, B. Anderson, J. Bradbury, A. DeGaetano, et al. 2007. Past and future changes in climate and hydrological indicators in the U.S. northeast. *Clim. Dyn.* 28: 381–407.
- Hewitson, B. C., and R. G. Crane. 1996. Climate downscaling: technique and application. *Clim. Res.* 7: 97–110.
- Hunter, M. D., and J. N. McNeil. 1997. Host-plant quality influences diapause and voltinism in a polyphagous insect herbivore. *Ecology* 78: 977–986.
- Inouye, D. W. 2008. Effects of climate change on phenology, frost damage and floral abundance of montane wildflowers. *Ecology* 89: 353–362.
- [IPCC] International Panel of Climate Change. 2007a. Summary for policymakers: 4th report. (<http://www.ipcc.ch/ipccreports/ar4-wg1.htm>).
- [IPCC] International Panel of Climate Change. 2007b. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (AR4). Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller (eds.), Cambridge University Press, Cambridge, United Kingdom and New York.
- Karl, T. R., and K. E. Trenberth. 2003. Modern Global Climate Change. *Science* 302: 1719–1723.
- Kilpatrick, A. M., M. A. Meola, R. M. Moudy, and L. D. Kramer. 2008. Temperature, viral genetics, and the transmission of West Nile virus by *Culex pipiens* mosquitoes. *PLoS Pathogen* 4: e1000092.
- Kiritani, K. 2006. Predicting impacts of global warming on population dynamics and distribution of arthropods in Japan. *Popul. Ecol.* 48: 5–12.
- Kunkel, K. E., H.-C. Huang, X.-Z. Liang, J.-T. Lin, D. Wuebbles, Z. Tao, A. Williams, M. C., J. Zhu, and K. Hayhoe. 2008. Sensitivity of future ozone concentrations in the northeast USA to regional climate change. *Mitig. Adapt. Strat. Glob. Change* 13: 5–6.
- Lafferty, K. D. 2009. The ecology of climate change and infectious diseases. *Ecology* 90: 888–900.

- Laird, A. K. 1964. Dynamics of tumor growth. *Br. J. Cancer* 18: 490–502.
- Logan, J. A., D. J. Wollkind, S. C. Hoyt, and L. K. Tanigoshi. 1976. An analytic model for description of temperature dependent rate phenomena in arthropods. *Environ. Entomol.* 5: 1133–1140.
- Logan, J. A., J. Regniere, and J. A. Powell. 2003. Assessing the impacts of global warming on forest pest dynamics. *Front. Ecol. Environ.* 1: 130–137.
- Lowry, W. P., and P. P. Lowry II. 1989. *Fundamentals of Biometeorology*, vol 1. Peavine Publications, Mc Minnville, OR.
- Luciani, M. A. 1987. The biology of the grape berry moth, *Endopiza viteana* (Clemens) (Lepidoptera: Tortricidae) in southern Ontario. M.S. Thesis, University of Guelph, Guelph, ON.
- Marshall, S. J., M. J. Sharp, D. O. Burges, and F. W. Anslow. 2007. Near-surface-temperature lapse rates on the Prince of Wales Icefield, Ellesmere Island, Canada: implications for regional downscaling of temperature. *Int. J. Climatol.* 27: 385–398.
- Martinson, T. E., C. J. Hoffman, T. J. Dennehy, S. J. Kamas, and T. Weigle. 1991. Risk assessment of grape berry moth and guidelines for management of the eastern grape leafhopper. New York's Food and Life Sciences Bulletin No. 138.
- Meehl, G. A., and C. Tebaldi. 2004. More intense, more frequent and longer lasting heat waves in the 21st century. *Science* 305: 994–997.
- Mills, E. 2005. Insurance in a climate of change. *Science* 309: 1040–1044.
- Nagarkatti, S., P. C. Tobin, and M. C. Saunders. 2001. Diapause induction in the grape berry moth (Lepidoptera: Tortricidae). *Environ. Entomol.* 30: 540–544.
- Nakicenovic, N., J. Alcamo, G. Davis, B. de Vries, J. Fenhann, S. Gaffin, K. Gregory, A. Grübler, T. Y. Jung, T. Kram, et al. 2000. Special report on emissions scenarios: an inter-governmental panel on climate change (IPCC) report. Cambridge University Press, Cambridge, United Kingdom.
- Naval Oceanography Portal. 2008. (<http://www.usno.navy.mil/>).
- Nietschke, B., R. D. Magarey, D. M. Borchert, D. D. Calvin, and E. Jones. 2007. A developmental database to support insect phenology models. *Crop Prot.* 26: 1444–1448.
- Northeast Climate Impacts Assessment [NECIA]. 2006. Climate Change in the US Northeast, Union of Concerned Scientists. Cambridge, MA. (<http://www.northeastclimateimpacts.org/>).
- Paaijmans, K. P., A. F. Read, and M. B. Thomas. 2009. Understanding the link between malaria risk and climate. *Proc. Natl. Acad. Sci. U.S.A.* 106: 13844–13849.
- Paaijmans, K. P., S. Blanford, A. S. Bell, J. I. Blanford, A. F. Read, and M. B. Thomas. 2010. Influence of climate on malaria transmission depends on daily temperature variation. *Proc. Natl. Acad. Sci. U.S.A.* 107: 15135–15139.
- Post, E. S., C. Pedersen, C. C. Wilmers, and M. C. Forchhammer. 2008. Phenological sequences reveal aggregate life history response to climatic warming. *Ecology* 89: 363–370.
- Pruess, K. P. 1983. Day-degree methods for pest management. *Environ. Entomol.* 12: 613–619.
- Raupach, M. R., G. Marland, P. Ciais, C. Le Quere, J. G. Canadell, G. Klepper, and C. B. Field. 2007. Global and regional drivers of accelerating CO₂ emissions. *Proc. Natl. Acad. Sci. U.S.A.* 104: 10288–10293.
- Reisen, W. K., Y. Fang, and V. M. Martinez. 2006. Effects of temperature on the transmission of West Nile virus by *Culex tarsalis* (Diptera: Culicidae). *J. Med. Entomol.* 43: 309–317.
- Riedl, H., and E. F. Taschenberg. 1984. Grape Berry Moth. Grape IPM Insect Identification Sheet No. 1. New York State Agricultural Experiment Station, Geneva, New York.
- Ruberson, J. R., K. V. Yeargan, and B. L. Newton. 2001. Variation in diapause responses between geographic populations of the predator *Geocoris punctipes* (Heteroptera: Geocoridae). *Ann. Entomol. Soc. Am.* 94: 116–122.
- Stinner, R. E., G. D. Butler, J. S. Bachelier, and C. Tuttle. 1975. Simulation of temperature-dependent development in population dynamics model. *Can. Entomol.* 107: 1167–1174.
- Tauber, M. J., C. A. Tauber, and S. Masaki. 1986. *Seasonal Adaptations of Insects*. Oxford University Press, New York.
- Taylor, F. 1981. Ecology and the evolution of physiological time in insects. *Am. Nat.* 117: 1–23.
- Tobin, P. C., S. Nagarkatti, and M. C. Saunders. 2001. Modeling development in grape berry Moth (Lepidoptera: Tortricidae). *Environ. Entomol.* 30: 692–699.
- Tobin, P. C., S. Nagarkatti, and M. C. Saunders. 2002. Diapause maintenance and termination in grape berry moth (Lepidoptera: Tortricidae). *Environ. Entomol.* 31: 708–713.
- Tobin, P. C., S. Nagarkatti, and M. C. Saunders. 2003. Phenology of grape berry moth (Lepidoptera: Tortricidae) in cultivated grape at selected geographic locations. *Environ. Entomol.* 32: 340–346.
- Tobin, P. C., S. Nagarkatti, G. Loeb, and M. C. Saunders. 2008. Historical and projected interactions between climate change and voltinism in a multivoltine insect species. *Glob. Change Biol.* 14: 951–957.
- Van Asch, M., P. H. van Tienderen, L.J.M. Holleman, and M. E. Visser. 2007. Predicting adaptation of phenology in response to climate change, an insect herbivore example. *Glob. Change Biol.* 13: 1596–1604.
- Wagner, T. L., H.-I. Wu, P.J.H. Sharpe, R. M. Schoolfield, and R. N. Coulson. 1984. Modeling insects development rates: a literature review and application of biophysical model. *Ann. Entomol. Soc. Am.* 77: 208–225.
- Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T.J.C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* 416: 389–395.
- Wing, S. L., G. J. Harington, F. A. Smith, J. I. Bloch, D. M. Boyer, and K. H. Freeman. 2005. Transient floral change and rapid global warming at the Paleocene-Eocene boundary. *Science* 310: 993–996.
- Yamamura, K., and K. Kiritani. 1998. A simple method to estimate the potential increase in the number of generations under global warming in temperate zones. *Appl. Entomol. Zool.* 33: 289–298.
- Zwiers, F., and G. Hegerl. 2008. Climate change: attributing cause and effect. *Nature* 453: 296–297.

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Appendix MATLAB code

% This code is made by MATLAB 2008a student version. Run and test under Ubuntu Linux 8.04.

% Further statistical analysis is made by R 2.10.1 under Ubuntu Linux 8.04.

%For any year:

%1 Read Photoperiod Data (Available)

data = csvread('photo.csv');

for i = 1:366

daytime = data(i,1:2); % read sunrise and sunset data

sunrise = daytime(1);

sunset = daytime(2);

minuterise = mod(sunrise,100); % convert into decimal

hourise = (sunrise-minuterise)/100;

minuteset = mod(sunset,100);

hourset = (sunset-minuteset)/100;

hours = hourset-hourise;

if minuteset>minuterise

minutes = minuteset-minuterise;

else

minutes = minuteset+60-minuterise;

hours = hours-1;

end

photoperiod(i) = hours+minutes/60; % calculate photoperiod

end

%2 Read Temperature Data (Daily Max/Min/Avg)

rawdata = csvread('until2050.csv'); % read raw temperature data

alltemp = reshape(rawdata,365,42); % make annual data

e1 = [];

e2 = [];

e3 = [];

e4 = []; % initiate each generation vector

gens = []; % initiate generations vector

for year = 1:42 % simulation throughout 2050

%initiate emergence time dataset

temperature = alltemp(1:365,year);

emergetime1 = [];

emergetime2 = [];

emergetime3 = [];

emergetime4 = []; % initiate emergence date vector

%Sub-model one Diapause Termination of first Generation

clear meanemerge1;

clear meanemerge2;

clear meanemerge3;

clear meanemerge4;

clear generation;

threshold = 8.4; % threshold

eggtemp = 75; % DD required for egg laying

for N = 1:10000

DD = 0;

day = 1;

termtemp = random('nbin',2,2/62)+148; %simulate a specific DD requirement for an individual using negative binomial distri.

while DD<termtemp % start DD accumulation

if temperature(day)>threshold

DD = DD+temperature(day)-threshold;

end

day = day+1;

end

t1 = day; % record current date

emergetime1 = [emergetime1 t1]; % put emergence time into dataset

%Egg laying times

Ddegg = 0; % initiate egg laying DD

while DDegg<eggtemp

if temperature(day)>threshold

DDegg = DDegg+temperature(day)-threshold;

end

day = day+1;

end

%Here completes first Generation, including Egg laying time

%Sub-model two Development (second Generation)

DD2 = 0;

devtemp2 = random('nbin',2,2/174)+250; %75 as DD required for egg deposition to complete one generation from egg to egg

while DD2<devtemp2 % DD required for second Gen. development

if temperature(day)>threshold

DD2 = DD2+temperature(day)-threshold;

end

day = day+1;

if day >364

break; % check if it exceeds the boundary

end

end

t2 = day;

emergetime2 = [emergetime2 t2];

%Egg laying times for gen 2.

DDegg2 = 0;

while DDegg2<eggtemp

if temperature(day)>threshold

DDegg2 = DDegg2+temperature(day)-threshold;

end

day = day+1;

if day >364

break;

end

end

eggdate = day; % record current day

%Here completes Second Generation, including Egg laying time

% What is the time now? Day? Notice the day is the time when the egg is laid.

night = 24-photoperiod(eggdate); % adjust to nightlength

basenight = 9.07; % This is what Tobin did.

if eggdate <197

choice = 1; % Choice one means continue development

elseif eggdate >234

choice = 0; % Choice 0 means going to diapause

else

```

change = night-basenight;
percent = 1-exp(-3.957*change); % Simulation
equation from Tobin
seed = random('unif',0,1); % Pick up a uniform RV
if seed<percent % Monte Carlo Simulation
choice = 0;
else
choice = 1;
end
end
end
% For the third Generation
if choice = = 1
DD3 = 0;
devtemp3 = random('nbin',2,2/174)+250;
while DD3<devtemp3
if temperature(day)>threshold
DD3 = DD3+temperature(day)-threshold;
end
day = day+1;
if day >364
break;
end
end
t3 = day;
emergetime3 = [emergetime3 t3];
%Egg laying times for the third generation
DDegg3 = 0;
while DDegg3<eggtemp
if temperature(day)>threshold
DDegg3 = DDegg3+temperature(day)-threshold;
end
day = day+1;
if day >364
break;
end
end
eggdate2 = day;
night2 = 24-photoperiod(eggdate2); % adjust to
nightlength
basenight = 9.07; %Tobin et al. 2003.
if eggdate2 < 197
choice2 = 1; % Choice one means continue devel-
opment
elseif eggdate2 > 234
choice2 = 0; % Choice 0 means going to diapause
else
change2 = night2-basenight;
percent2 = 1-exp(-3.957*change2); % Tobin et al.
2003
seed2 = random('unif',0,1); % Pick up a uniform RV
if seed2<percent2% Monte Carlo Simulation
choice2 = 0;
else
choice2 = 1;
end
end
if choice2 = = 1
DD4 = 0;
devtemp4 = random('nbin',2,2/174)+250;
while DD4<devtemp4
if temperature(day)>threshold
DD4 = DD4+temperature(day)-threshold;
end
day = day+1;
if day >364
break;
end
end
t4 = day;
emergetime4 = [emergetime4 t4];
end
end
meanemergetime1 = mean(emergetime1);
meanemergetime2 = mean(emergetime2);
meanemergetime3 = mean(emergetime3);
meanemergetime4 = mean(emergetime4);
e1 = [e1 meanemergetime1];
e2 = [e2 meanemergetime2];
e3 = [e3 meanemergetime3];
e4 = [e4 meanemergetime4];
% caculate # of generations in one simulation
generation = size(emergetime(4,2))*4/10000+
(size(emergetime(3,2))-size(emergetime(4,2)))*3/
10000+(1000-emergetime(3,2))*2/1000
gens = [gens,generation];
end
end
end
e1
e2
e3
e4
gens

```