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Abstract. Understanding the effects of environmental variation on insect populations is important in light of predictions about increasing climatic variability. This paper uses the univoltine western corn rootworm (WCR, *Diabrotica virgifera virgifera* LeConte) as a case study and employs deterministic and stochastic modeling to evaluate how insect population dynamics is shaped by density-dependent survival and annual variation in temperature, which are key in regulating insect populations. Field data showed that larval survival varied significantly between years but was constant for a range of densities. Survival dropped only beyond a threshold density, a feature resembling generalized Ricker functions used in modeling density-dependent survival due to scramble competition for resources. We used soil temperature data for 20 yr to model annual variation in developmental time and survival. The deterministic model, where the developmental time was same across years, showed that though survival was high and did not change for a range of densities (i.e., density-independent survival), predicted densities were large enough that strong density dependence could occur in the field (i.e., predicted densities fall in the region where survival drops sharply) and that populations could exhibit stable equilibrium, cycles, etc. Interestingly, populations with lower density-independent survival were less likely to produce stable equilibrium compared to populations with higher density-independent survival. We found that population densities were at stable equilibrium when both mean developmental time and fertility were relatively low or when developmental time and fertility were relatively high. This in turn implies that, in warmer regions, where mean developmental time will be lower, stability is more likely for insect populations with low fertility; species in warmer regions will experience cyclical and unstable dynamics when fertility is high. While increase in the mean developmental time reduces overall survival, increasing variation in developmental time could increase mean survival, a consequence of the Jensen's inequality, since survival was a concave decreasing function of developmental time. Hence, both mean and variability in temperature affect the dynamics of insect populations. Finally, we found that stochastic variation in soil temperature produced large variation in predicted population densities that could potentially enhance or diminish the effect of density dependence.

Key words: climate change; degree-days; density dependence; *Diabrotica virgifera virgifera* LeConte; environmental variation; generalized Ricker function; population dynamics.

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INTRODUCTION

Two important factors influencing population dynamics of insects and other poikilothermic organisms are temperature and density dependence in vital rates such as fertility, survival, and developmental time (Varley et al. 1973). The strong relationship between temperature and insect development has led to the degree-days concept, which predicts developmental time based on the total amount of heat accumulated that falls within the species-specific lower and upper temperature thresholds (Wilson and Barnett 1983). While degree-day models work well for predicting developmental time under constant temperatures, temporal variation in temperature can produce variation in developmental time and hence can have important consequences for population dynamics (Boyce et al. 2006). While the effects of demographic stochasticity and individual-level variation in developmental time due to availability and quality of resources on population dynamics have been analyzed in some studies (e.g., Blythe et al. 1984, Plant and Wilson 1986, Briggs et al. 1993, Wearing et al. 2004), effects of abiotic factors, especially the effects of variation in temperature on insect population dynamics have only rarely been explicitly incorporated in population models. Bannerman and Roitberg (2014) investigated impacts of extreme temperatures in a host–parasitoid system using a cyclical sinusoidal temperature model (variation between night and day temperatures); Amarasekare and Coutinho (2013) included effects of seasonal variation in temperature on population growth, also using a cyclical temperature model. It is critical to understand the population level effects of stochastic temperature variation because climate models predict not only changes in means but also variability in temperature (Helmuth et al. 2002).

In addition to temperature, density dependence is a key component of insect population dynamics (Gutierrez 1996). The dynamics of density-dependent models can be complex even in the absence of environmental variation. Whether models predict stable (reaching asymptotic population size via a monotonous increase or damped oscillation) or unstable dynamics (limit cycles or chaos) depends on the life-history parameters. Further, the functional form of density dependence affects predicted population dynamics (Juliano 2007). For instance, density dependence in survival can be modeled as an exponentially decreasing function (Hassell 1975), which assumes that survival is affected even when density is relatively low. This form of density dependence can occur, for instance, in the presence of cannibalism (e.g., pupal cannibalism by adults in *Tribolium* spp., Costantino et al. 1997), where each increase in population size increases the encounter rate and hence the frequency of cannibalistic interactions. However, survival might also be impacted by resource limitation rather than cannibalism as in the tobacco beetle (*Lasioderma serricorne*, Bellows 1981) or in the healthy or parasitized larvae of *Ephestia kuehniella* (Bernstein et al. 2002) where the larval-to-adult survival decreases only if larval density exceeds some threshold value. Variation in temperature could enhance or diminish the effect of density dependence by affecting population densities. For instance, temperature could affect insect vital rates independently of density or could affect density by directly affecting the resources (e.g., food supply) for insects. In the former case, if daily density-dependent larval survival is independent of temperature (e.g., Régnière et al. 2012), then overall survival in a season would be determined by the number of days to complete the larval stage. Models integrating empirical information of such interactions between temperature and density dependence are rare, though it is known that variation in abiotic factors can affect population dynamics (Lande et al. 2003, Haridas et al. 2015).

In this work, we used field data and deterministic and stochastic population models to address three issues: firstly, we seek to understand population dynamics when survival is reduced only at large densities. If survival is reduced only when density exceeds some threshold value, it is natural to ask how population densities are regulated through density dependence. To address this issue, we developed deterministic models to predict densities of overwintering eggs and larvae that help in understanding the strength of density dependence. Secondly, we investigate how mean developmental time affects the dynamics (i.e., stable equilibrium, cycles, etc. in a constant environment) of insect populations. Since developmental time is determined by temperature,

changes in temperature due to climate change could affect stability of insect populations. Lastly, we ask how annual variation in soil temperature affects larval survival and hence larval densities. Variation in larval densities could affect the strength of density dependence and hence has consequences for population dynamics. Further, prediction of variation in larval densities due to environmental stochasticity is critical in devising pest management strategies. We used the univoltine western corn rootworm (WCR, *Diabrotica virgifera virgifera* LeConte), one of the most serious crop pests in North America (Vidal et al. 2005) and the focus of intense pest management efforts (Meinke et al. 2009), as a case study. The advantage of using an economically important species is that good data and parameter estimates are often available in the literature. To generalize the model predictions to a wide range of insect species, we explored how variation in model parameters (e.g., density-independent survival, fecundity, and mean developmental time) affected model outcomes. The WCR lives its juvenile stages (eggs, larvae, pupae) in the soil, and the larval stage causes the most damage to the plant. We used an infestation study conducted in 2005 and 2007 to quantify the egg-to-adult survival relationship in the field for a large range of initial egg densities (Hibbard et al. 2010). Further, we used annual soil temperature records for 20 yr (1994–2013) from a location close to the experimental site to estimate annual variation in developmental time using degree-days for the development of WCR larvae. The deterministic and stochastic population models we develop here help in integrating density dependence and temporal environmental variation to study insect population dynamics.

METHODS

Modeling density-dependent survival

We used adult emergence data from a field study by Hibbard et al. (2010) which was conducted at the University of Missouri Bradford Research and Extension Center, 9 km east of Columbia, Missouri, USA. They measured the percentage of adult emergence in the field at seven egg infestation levels, D (25, 50, 100, 300, 600, 1200 and 2400 eggs per rows of length 30.5 cm, with 1.6 plants per row), during
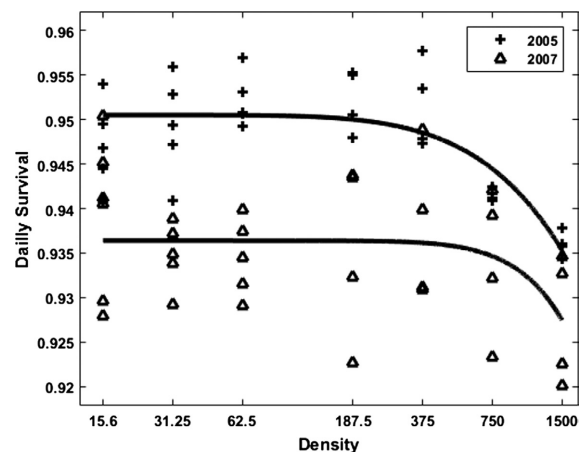

Fig. 1. Daily survival in 2005 (+) and 2007 (Δ) plotted against the seven egg infestation levels (15.6, 31.3, 62.5, 187.5, 375, 750, and 1500 eggs per plant) plotted on logarithmic scale. Daily survival was obtained by converting the total survival (from egg to adult stage) rates reported in Hibbard et al. (2010).

April–July in 2005 and in 2007. In both years, egg to adult survival decreased only at high egg infestation levels, but in 2005, the maximum density-independent survival (at low densities) was ≈8.4% while in 2007, the maximum survival was only ≈2.4%. To model the effect of temperature on adult emergence, we used the degree-days to convert the emergence percentages into daily survival rates as $p_d = P^{\frac{1}{DT}}$, where p_d is the daily survival rate, P is the proportion of emerging adults, and DT is the number of calendar days to complete development from egg to adult stage. We estimated DT by adding the mean daily soil temperature (http://agebb.missouri.edu/weather/stations/boone/index.html) that were above the developmental threshold of 11.1°C (Wilde 1971, Levine et al. 1992) from May 19 in 2005 and May 8 in 2007 (infestation dates) until 700 degree-days were reached (Hibbard et al. 2010). DT was 50 d in 2005 and 55 d in 2007. We repeated this procedure for each infestation level in 2005 and 2007 (Fig. 1) and estimated daily density-dependent survival (p_d) using nonlinear regression analysis. The dependent variable was daily survival p_d and the independent variable was the logarithm of egg density D per plant. The daily survival was explicitly given by the function

$$p_d = \exp\left(-\left(a\left(\log(D) - \log\left(\tfrac{25}{1.6}\right)\right)\right)^b\right) - c, \text{ where}$$

$a = 0.10434$, $b = 5.6321$, $c = 0.0495$ in 2005, and $a = 0.13627$, $b = 9.927$, $c = 0.0636$ in 2007. The lowest density per plant was 15.6 eggs (= 25 eggs/1.6 plants) and the parameter c determines the average density-independent survival ($1 - c = 0.9505$ in 2005, and $1 - c = 0.9364$ in 2007) at low densities. Hibbard et al. (2010) estimated critical densities (≈532 over-wintering eggs per plant in 2005 and ≈707 over-wintering eggs per plant in 2007), only above which density dependence reduced the survival. The parameters a and b determine the strength of density dependence, and the difference in these parameters between 2005 and 2007 corresponds to the difference in critical densities. Temperature can influence adult emergence via developmental time such that individuals experiencing cooler temperatures are exposed to larval specific mortality for a longer period of time. Aside from this effect on developmental time, results from Jackson and Elliott (1988) showed that temperature did not influence daily larval mortality in WCR unless temperature exceeded 32°C during the developmental period. Note that adult emergence rates reported in Hibbard et al. (2010) could be affected by factors other than temperature including predation and parasitism, especially at low densities (Onstad et al. 2006). Hence, non-temperature factors account for the difference in daily survival rates p_d between 2005 and 2007.

Incorporating annual variation in soil temperature

We used soil temperature data from St. Joseph, MO, which is close to the site of the field studies of Hibbard et al. (2010); these data were available from the High Plains Regional Climate Center at the University of Nebraska-Lincoln (http://www.hprcc.unl.edu/). We calculated the number of days, DT, to complete the development from egg to adult stage for 20 yr (1994–2013), assuming eggs started to be sensitive to temperature on May 15 (Fig. 2a). Soil temperature data at St. Joseph, Missouri, USA, showed that during 1994–2013, there were only 8 d (7 d in 2005 and 1 d in 2012; less than 1% of the total number of days) when temperature was above 32 °C during the study period. The
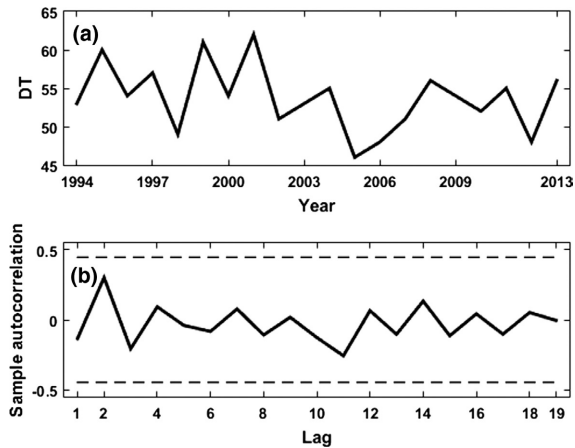

Fig. 2. (a) Calendar days DT required for completing 700 degree-days at St. Joseph, MO, USA. Soil temperatures were recorded at 10.16 cm (4 in.) and are available from the High Plains Regional Climate Center at University of Nebraska-Lincoln (http://www.hprcc.unl.edu/). (b) Sample autocorrelation of DT values plotted against lags of length 1–19. Dashed lines correspond to critical values (±0.4472) beyond which autocorrelations are significant.

density-dependent survival over the entire juvenile stage in year t was modeled as $p(t) = \exp(-1(1 - p_d)DT(t))$, where p_d was obtained from the density-dependent function described above and $DT(t)$ is the developmental time in year t. Here, we assume that mortality is multiplicative and is the same for each day and that temperature affects survival only through its effects on DT. Note that larval survival is a convex decreasing function of developmental time DT.

Deterministic and stochastic population models

We tracked larval densities using a population model given by the equation

$$L_t = L_{t-1} \times w_{t-1}, \tag{1}$$

where L_t denotes the larval density per plant in year t, and L_{t-1} is the population growth rate (or fitness) given by

$$w_{t-1} = p(t-1) \times f, \tag{2}$$

where $f = F \times p_E$ is the per capita number of overwintering eggs, F is the per capita number of female eggs, and p_E is the overwintering

survival rate of eggs. Note that the density of over-wintering eggs per plant in year t is given by $L_{t-1}f$ and hence the overall density-dependent survival $p(t)$ is a function of larval density since the daily survival p_d can be expressed as

$$p_d = \exp\left(-\left(a\left(\log\left(\frac{L_t f}{15.6}\right)\right)\right)^b\right) - c.$$

For the WCR, we assumed a baseline per capita fertility of 220 eggs, a sex ratio of 0.5, and an overwintering mortality of 0.5 (Onstad et al. 2001). For the deterministic model, we assumed that there was no annual variation in egg-to-adult developmental time and that DT was given by the average value during 1994–2013 (Fig. 2a; mean of DT = 53.75 d). We also assumed that the density-dependent survival p_d was either always as in year 2005 or was always as in year 2007 (Fig. 1). The deterministic model was analyzed by iterating Eq. 1 for 50,000 time units using an initial density of 15.6 larvae per plant.

We incorporated stochasticity in two ways: in the first case, we assumed that both DT p_d and the daily survival p_d were random. We did not detect any autocorrelation in DT values (Fig. 2b) and hence we assumed that DT varies randomly between years (i.e., each DT value displayed in Fig. 2a, occurs with probability = 1/20). The daily survival p_d could be either that of 2005 or that of 2007 with equal (= 1/2) probability. By varying p_d between 2005 and 2007, we account for stochasticity due to non-temperature factors and take into consideration the variation in density-dependent parameters between years. In the second case, we assumed that DT was fixed (i.e., annual variation in soil temperature does not affect survival), but that p_d could be either that of 2005 or that of 2007 with equal (= 1/2) probability. Using the two models, we could compare the effect of variation in temperature to variation in other factors affecting survival on population dynamics. Analyses of both stochastic models were carried out by iterating Eq. 1 for 50,000 time units and repeating the iterations 300 times to produce probability distributions of larval densities.

RESULTS

Deterministic simulations

The predicted population dynamics strongly depended on the per capita fertility F (Fig. 3): the population went extinct (of the order of 10^{-300}), when F was very low (<30 for 2005 and <60 for 2007); as F increased larval density, L^*, reached a non-zero stable equilibrium, which first increased and then decreased with higher values of F (Fig. 3a). For parameters that result in stable equilibrium, the equilibrium density of the deterministic model is explicitly given by

$$L^* = \left(\frac{15.6}{f}\right)\exp\left(\frac{J}{a}\right), \quad (3)$$

where, $J = (-\log(J_1))^{\frac{1}{b}}, J_1 = 1 + c - \log\left(f^{\frac{1}{DT}}\right)$, and a, b, and c are the coefficients of the daily density-dependent survival function p_d in 2005 and 2007 (see Appendix S1). In equilibrium, the total number of over-wintering eggs per plant is given by L^*f, which is a measure of the strength of density dependence experienced by the hatching larvae. Note that f is the number of overwintering eggs produced by a single female larva. When fertility F was low, the total number of over-wintering eggs was low (Fig. 3b) and larvae experienced weak density-dependence; as F increased, the total number of over-wintering eggs increased leading to stronger density dependence (arrows in Fig. 3b), and as a result, larval density L^* decreased (Fig. 3a). As F increased further (>190 for 2005 and >160 for 2007), larval densities started exhibiting cycles (of periodicity 2, 4, 8, …, generations) and eventually became unstable and chaotic as illustrated using the bifurcation diagrams for 2005 and 2007 (Fig. 4). In particular, the deterministic models predicted cyclical larval densities for the western corn rootworm when the baseline per capita fertility was 220 eggs (Onstad et al. 2001).

Fertility F and the maximum density-independent larval survival $1-c$ influenced the nature of long-term population dynamics (Fig. 5). The population went extinct when both, maximum survival and F were low; as maximum survival and F increased densities reached a stable equilibrium; for larger values of F and
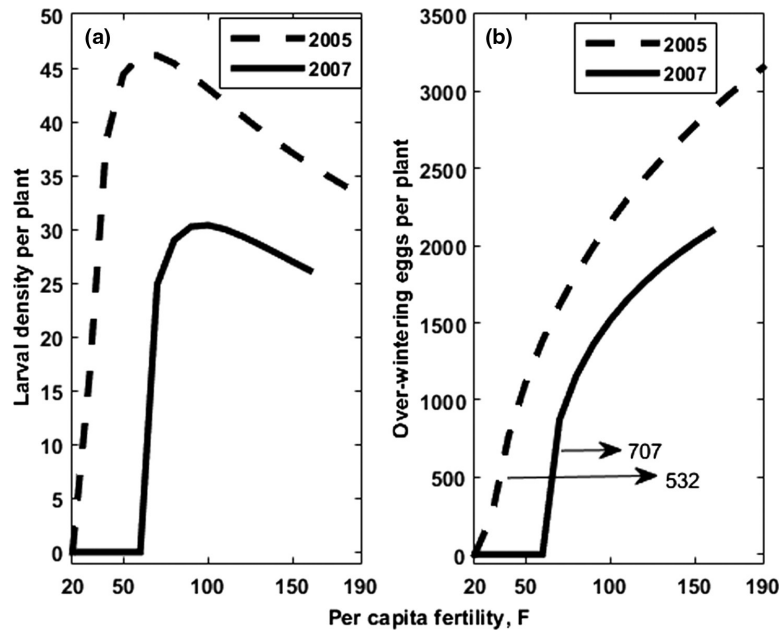
Fig. 3. (a) Larval densities at equilibrium predicted by the deterministic models as a function of the per capita fertility of females F; the population goes extinct when $F < 30$ if p_d is based on 2005 and <60 if p_d is based on 2007 and show stable equilibrium when F is approximately <190 if p_d is based on 2005 and <160 if p_d is based on 2007. (b) Predicted over-wintering eggs per plant when the deterministic models show a stable equilibrium; arrows indicate the number of eggs estimated by Hibbard et al. (2010) (converted here to per plant) above which density-dependent mortality occurred in the field.
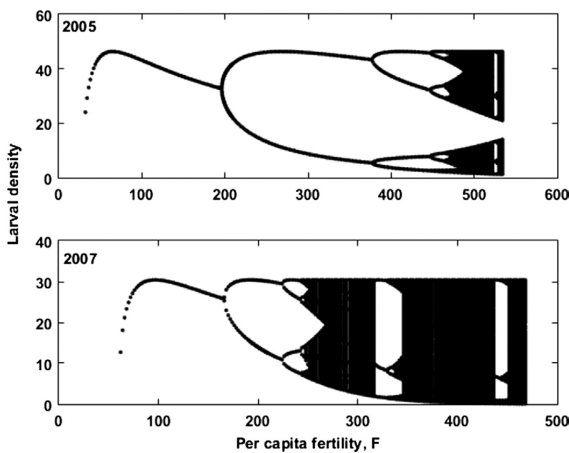

Fig. 4. Bifurcation diagrams showing the dynamics of larval densities per plant for different values of per capita fertility of females, F. Densities show stable equilibrium for low values of F before bifurcating into cycles and eventually become unstable when F is large.

maximum survival $1 - c$, population densities first showed cyclical behavior before bifurcating into unstable dynamics. The parameter region (i.e., values of F and $1 - c$) determining stable and unstable equilibrium differed between 2005 and 2007: for a given survival rate $1 - c$, there were more fertility values in 2005 that produced a stable equilibrium. In general, all parameters of the model determined model stability: the condition for stability is given by (see Appendix S1)

$$\left|1 + \left(\frac{1}{J}\right) ab\, DT\, J_1 \log(J_1)\right| < 1. \qquad (4)$$

Hence, all parameter combinations that makes the left hand side of the expression in Eq. 4 smaller than 1, produce a stable equilibrium. The stability in particular depended on the mean time (DT) to develop from egg to the adult stage and hence depended upon the soil temperature.
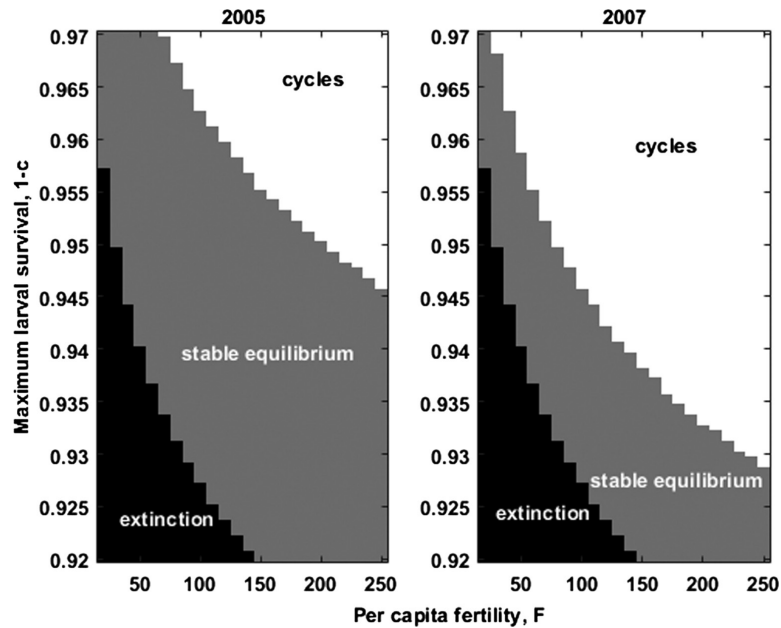
Fig. 5. Different dynamics of larval densities shown by the deterministic models for 2005 and 2007 for different values of the survival at low densities ($1 - c$, y-axis) and per capita fertility of females, F.
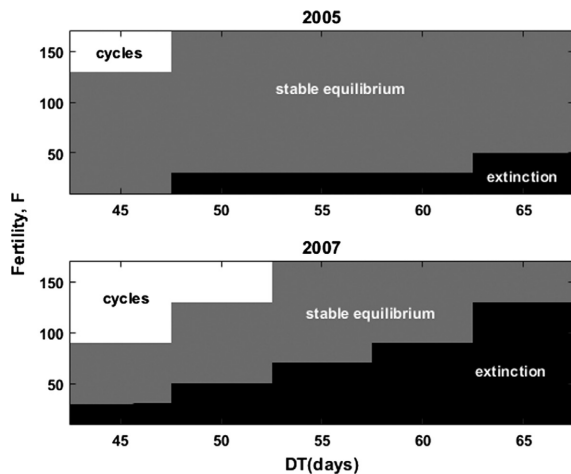

Fig. 6. Stability of larval densities for different values of mean developmental time DT and per capita fertility, F. Density-dependent survival for 2005 and 2007 are as given in Fig. 1. Parameter regions corresponding to cycles represent cycles of periodicity 2.

When DT is high stability is achieved even when fertility rates are high; when DT is low stability is achieved only when fertility is relatively low (Fig. 6). High fertility and low developmental time result in cyclical and unstable chaotic dynamics. Note that a low developmental time DT would imply higher survival since survival is multiplicative.

Stochastic simulations

The stochastic model predicted large variation in larval density (Fig. 7). For instance, when per capita fertility F was 220 and overwintering mortality was 0.5, as was the case for the western corn rootworm (Onstad et al. 2001), stochastic simulations showed that larval densities can vary from a low of 0.0115 larvae per plant to a high of 72 larvae per plant (Fig. 7a). The corresponding deterministic predictions from 2005 result in a two-point cycle that fluctuates between 19 and 44 larvae per plant while the deterministic prediction from 2007 result in a two-point cycle of 11 or 30 larvae per plant (arrows in Fig. 7a). The average population density from the stochastic model (= 21.1 larvae per plant) was less than that predicted by the deterministic model (= 25.8 larvae per plant) in which survival was assumed to be the average of 2005 and 2007 values and developmental time was the same (53.75 d) for every year. A further simulation, where only the survival rates varied between 2005 and 2007
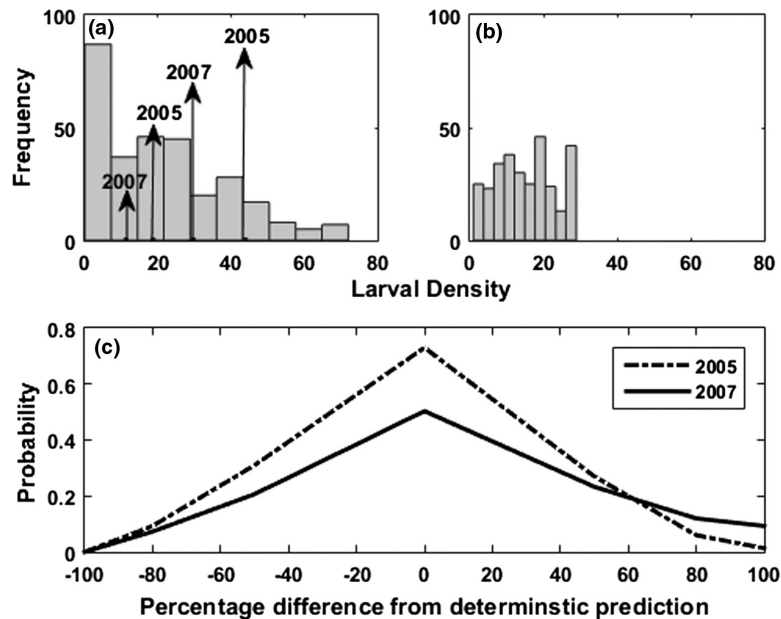
Fig. 7. (a) Histogram of the larval density from 300 simulations of the stochastic model where both survival and developmental time are random when per capita fertility, $F = 220$ and overwintering mortality $p_E = 0.5$. Arrows indicate equilibrium densities predicted by the deterministic models using larval survival p_d from 2005 to 2007 as in Fig. 1. (b) Histogram of the larval density from 300 simulations of the stochastic model where only survival is varied between 2005 and 2007 values randomly but developmental time is fixed at its 20-yr average. Per capita fertility, $F = 220$ and overwintering mortality $p_E = 0.5$. (c) Probability that predictions from the stochastic model (when per capita fertility, $F = 220$ and overwintering mortality $p_E = 0.5$) differ from the highest density predicted by the deterministic model using survival estimates from 2005 to 2007. Positive values indicate that in any given year populations are larger than expected from the deterministic model.

(and not the soil temperature), showed that variation due to temperature had a larger effect on larval densities (Fig. 7b). The stochastic model helps in predicting probabilities that larval densities are above or below specific thresholds: for instance, probability that larval density is less than the deterministic predictions in 2005 or 2007 varies from 50 to 97%. There is ≈60% chance that larval densities are 20% more than the highest density predicted by a deterministic model using the survival rates of 2005 (Fig. 7c).

Discussion

Understanding the effects of environmental variation on insect population dynamics is important in light of predictions of increasing climatic variability (Meehl and Tebaldi 2004). Even though stochastic models are increasingly being used in ecology to understand the

persistence of several species (Boyce et al. 2006), predictions about insect population dynamics are mostly based on deterministic models using laboratory measurements in simplified (constant) environmental conditions (Kingsolver et al. 2011). Since density dependence is documented to be an important factor in regulating insect population densities (Gutierrez 1996), it is necessary to integrate density-dependent vital rates with stochastic environmental variation in insect population models. In this work, we developed a population model to study how density-dependent survival observed in the field and stochastic variation in soil temperature influence the population dynamics of a univoltine insect. We used field data on the western corn rootworm which showed that survival was reduced only when density reached relatively large levels (Fig. 1), suggesting negligible effects of density dependence (Hibbard et al. 2010).

However, when this density-dependent survival was used in a deterministic population model, we found that densities of overwintering eggs could be large enough (unless overwintering survival and/or fertility is very low) that strong density dependence could occur in field populations (Fig. 3b). This emphasizes the importance of accurate quantifying of density dependence in field conditions at varying densities and of developing models to understand how the observed relationship between density and a vital rate affects population dynamics. When stochastic variation in soil temperature was included in the model, we observed large variation in the predicted annual larval density (which in turn determines the density of overwintering eggs in the next season), showing that environmental variation can either enhance or diminish the strength of density dependence. Our model assumed that temperature affected overall survival only through effects on developmental time, an assumption that was based on laboratory studies of WCR by Jackson and Elliott (1988). This assumption has been demonstrated in a wide range of insects including the eastern spruce budworm *Choristoneura fumiferana* (Clem.), the spruce budmoth *Zeiraphera canadensis* Nutuua and Freeman (Lepidoptera: Tortricidae), the melon fly *Bactrocera cucurbitae* (Coquilett) (Diptera: Tephritidae), the mountain pine beetle *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae, Scolytinae), and the western spruce budworm *C. occidentalis* Freeman (Lepidoptera: Tortricidae) (Régnière et al. 2012). The effect of variation in temperature on population densities calls for long-term field monitoring of larval/adult densities to evaluate how environmental variation affects density-dependent insect population dynamics.

The specific density-dependent functional relation derived here is similar to the generalized Ricker functions and is consistent with density-dependent mortality due to scramble competition for resources (Pomerantz et al. 1980, Thomas et al. 1980, Bellows 1981, Bernstein 1986). This density–survival relationship has been used to model survival in laboratory populations of *Tribolium castaneum* (Herbst.), *Tribolium confusum* Duval and *Lasioderma serricorne* (F.) (Bellows 1981). Bernstein et al. (2002) used generalized Ricker functions to model survival of healthy as

well as parasitized (by *Venturia canescens*) larvae of *Ephestia kuehniella* in a host-parasitoid system. In comparison to Bernstein et al. (2002), the higher values of the parameter b and lower values of the parameter a (which correspond to parameters θ and α, respectively, in Bernstein et al. 2002) in our case describe survival that is higher but constant (density-independent survival) over a large range of densities and drops sharply only at higher densities (Fig. 1).

The dynamics of the deterministic density-dependent model depends on the parameter values in the model. The cycles (and chaotic dynamics) result from the overcompensatory nature of survival (modeled by the generalized Ricker functions) where higher survival at lower densities leads to an increase in density. Density dependence then results in a reduction in density in the following generation thus producing cycles (Murdoch et al. 2003). For species with larger number of over-wintering eggs (equivalently larger per capita fertility or over-wintering survival) and lower density-independent mortality, one would expect cycles and unstable dynamics (Fig. 5). Increase in the intrinsic population growth rate, due to higher survival and/or fertility, leads to unstable dynamics in discrete time density-dependent models (Gotelli 2001). However, note that the stability region produced using the survival in 2005 was considerably larger than that used the survival in 2007 even though density independent larval survival $(1 - c)$ in 2005 was relatively high. This is because a high density-independent larval survival increases competition for resources resulting in stronger density-dependent regulation as indicated by a smaller threshold density in 2005 beyond which larval survival decreases (Hibbard et al. 2010, Fig. 1).

We showed that the stability of the model depended on temperature through its effect on the average developmental time (Eq. 4). In particular, in warmer regions, where this average will be lower, stability is more likely for species when density of over-wintering eggs is relatively low; species in warmer locations will experience cyclical and unstable dynamics when density of over-wintering eggs is high. While increase in the mean developmental time reduces overall survival, increasing variation in developmental time could increase mean survival, a consequence of

the Jensen's inequality (Ruel and Ayres 1999) since survival is a convex decreasing function of developmental time. This suggests that the dynamics (stability, cycles, etc.) of insect population densities depend on both the mean as well as the variation in temperature, which is similar to the findings in Vasseur et al. (2014) and Estay et al. (2014).

Our use of time series data on temperature combined with the concept of degree-days for development provide a novel tool in pest management: in the case of an agricultural pest like the WCR, our model could be used to predict probabilities of larval densities being above or below an economic injury threshold (e.g., Fig. 7c). Mitchell and Riedell (2001) used a stochastic model for the northern corn rootworm (*Diabrotica barberi* Smith & Lawrence) that included plant phenology and a different form of density dependence, but did not study the consequences of nonlinear dynamics. Larval densities predicted by our stochastic models show considerable variation that is obscured by deterministic predictions and hence field monitoring of densities might be important in management of pests in light of increasing climatic variability.

To summarize, we demonstrated how density-dependent survival modeled by a generalized Ricker function where survival is affected only at relatively large densities, affects the population dynamics of insects and how this dynamics could be affected by temporal stochastic variation in an environmental driver like temperature. Climate models predict changes in both the means and the variability of temperature (Helmuth et al. 2002), and changes in climate affect the distribution and abundance of several insect species (Paaijmans et al. 2013) with warmer temperatures generally leading to higher survival and more rapid development in insects in mid to high latitudes (Stange and Ayres 2010). Since temperature responses of several vital rates, including mortality are determined by underlying biochemical processes and are known to be similar across many insect taxa (van der Have 2002, Kingsolver 2009), our results provide a general modeling framework that integrates density dependence and temporal environmental variation in insect vital rates that could be used in testing these predictions of the potential impacts of climate change.

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