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Optimizing insecticide timings for the grape mealybug, *Pseudococcus maritimus* (Hemiptera: Pseudococcidae) based on pheromone trap capture data

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In agricultural systems, insect pest populations are often assessed using traps to survey adults, as adults are mobile and attracted to volatiles. While immature stages of insects (nymphs, larvae) are often most damaging, they can be difficult to sample, and management decisions targeting immatures must be based on adult sampling. For some insect pests, such as the grape mealybug (*Pseudococcus maritimus*), pheromone trap observations of adults occur too late to warn growers about pest risk, since overwintering first-instar nymphs are the dominant stage that transmits grape leafroll-associated viruses. Here, we propose a method to determine the time when insecticide applications will be most effective to control first-instar grape mealybug nymphs, based on the alignment between a modeled progression of life stages across degree days and pheromone trap capture data. We used literature to build a grape mealybug phenology simulation model and a 6-yr dataset of grape mealybug males captured in pheromone traps to infer the time when most virus-transmitting nymphs have hatched and are susceptible to insecticides. Our results show it is unlikely that most overwintering first-instar grape mealybugs occur in early spring, and that insecticides aimed at preventing grape leafroll-associated viruses transmission should occur by late autumn. Our study suggests that results from laboratory studies and field observations can be integrated to optimize insecticide application timing for a key vector pest species.

Keywords: grape mealybug, insect monitoring, phenology models, pheromone, trap captures

Introduction

Decision-making in integrated pest management often relies on monitoring using pheromone traps that target mobile life stages of pests, even when those stages may not be directly harmful to crops. The idea of pest monitoring is to use data from adult captures to gauge pest pressure, forecast damage, and decide when and where to use insecticides or other pest control tactics effectively (Prasad and Prabhakar 2012). However, for many pests, insecticides target immature stages that are difficult to sample and rarely captured in traps, and the windows when these insecticide sprays are most effective at reducing pest populations are often missed (eg, Walker et al. 1990, Nault and Kennedy 1996, Mermer et al. 2021). For instance, when applications are timed to maximum egg hatch, they may result in pest reductions close to 100%, but expected mortality decreases as applications miss key phenological events (Jones 2021). Unfortunately, optimal timing can only be guessed when it is solely based on information collected from pheromone traps without considering pest phenology.

Phenology models predict the proportion of pest individuals in a life stage based on degree-day accumulation after a biofix (Damos 2015). These models are most often developed from data collected in laboratory studies that measure insect development as a function of temperature, which are used to simulate phenology timing and its variability through systems of differential equations (Jones et al.

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2010, Tonnang et al. 2017). Phenology models are then calibrated and validated with field data from several locations and years to guide pest management strategies by predicting the first, peak, and last occurrence of stages or the transitions from one stage to the next (Welch et al. 1981). However, while phenology models are widely used to optimize timing of pesticide applications, they are rarely linked directly with pest monitoring networks to make decisions (Jones et al. 2010). Linking phenology models with real-time trap capture data may be the key to more effective decision making in agroecosystems (Rincon et al. 2024).

The grape mealybug, *Pseudococcus maritimus* (Ehrhorn) (Hemiptera: Pseudococcidae), is a major vector of grape leafroll-associated viruses (GLRaVs), the causal agents of grape leafroll disease, the most destructive viral disease in wine grapes. The grape mealybug and the associated GLRaVs can cause up to 60% yield loss and is present in all major grape-growing regions in the world (Almeida et al. 2013, Naidu et al. 2014, O'Hearn and Walsh 2021). The grape mealybug usually completes 2 generations per year, overwinters as eggs or first-instar nymphs and all life stages are sessile and feed on grapevine phloem, except for adult males that can fly, and first and second instar nymphs that can crawl between and feed from different vine grape plants (Geiger and Daane 2001, Daane et al. 2012). Most GLRaVs are transmitted by grape mealybug first and second instar nymphs (Grasswitz and James 2008, Daane et al. 2012) and growers use delta traps baited with grape mealybug sex pheromone to gauge control treatments with systemic insecticides aimed to kill first-instar nymphs and minimize GLRaVs spread (Bahder et al. 2013, O'Hearn and Walsh 2020). However, the timing of insecticide applications can only be guessed from field observations and mainly based on the seasonal vine grape plants' capacity to uptake and transport systemic insecticides (O'Hearn and Walsh 2020).

Here we use field data and simulation modeling to predict when most grape mealybug first-instar nymphs (ie, crawlers) hatch and are actively moving between crop plants, and we use these predictions to gauge when insecticide applications will be most effective at preventing the spread of GLRaVs. We use a system of differential equations to simulate the progression of grape mealybug phenology across degree days and propose optimal insecticide timing based on the alignment between model outputs with field-collected pheromone trap captures. Beyond grape mealybug, our approach can be applied to other pests where field data are collected at regular intervals and phenology can be modeled based on annual heat accumulation. We show that the combined analysis of phenology parameters and field data is useful to determine the time window when the application of control treatments is most efficient, especially for pests like the grape mealybug whose most damaging stage is cryptic and hard to sample.

Materials and Methods

Field Data Collection

Sex pheromone lures for *P. maritimus* were obtained from Trécé Inc. (Adair, OK, USA) and Dr. Jocelyn Millar at University of California, Riverside. These lures consisted of 25 µg of encapsulated pheromone in a 25 µL hexane solution within 11 mm diameter gray silicon rubber septa (West Pharmaceuticals, Lititz, PA, USA). Lures were deployed in delta traps placed under the vine canopy in the middle of wine grape and Concord grape vineyards located in Paterson, Prosser and Roza, WA, USA. Vineyards were sampled weekly by registering the number of males captured in 144 traps in 2009, 195 in 2010, 78 in 2011, 4 in 2021, 10 in 2022, and 12 in 2023 (6 yr total) (Fig. 1). Traps were maintained from early May, when the first flight was observed, until late October, when no flights were observed, for all years.

Daily minimum and maximum temperatures for each year and site were sourced from the nearest Washington State University AgWeatherNet station (https://weather.wsu.edu/). Degree days were calculated using the single sine method (Baskerville and Emin 1969) assuming a lower temperature threshold of 10 °C (Geiger and Daane 2001) and an upper threshold of 29.8 °C (Dixon et al. 2009) with a horizontal cutoff.

Model Development

A simulation model for grape mealybug was constructed to determine the timing of life stages across 2 generations (Fig. 2). We used a dynamic systems approach, where populations are modeled using state and rate variables connected by flow channels (Forrester 1965). State variables represent insect life stages, fecundity and development were rate variables that control flows in and out of the system (population) and between life stages, and migration and mortality rates were assumed to be negligible. The value assigned to state variables is updated each time step by integrating simultaneously the product of rate variables and the last value assigned to the connected state variables (Tonnang et al. 2017) (Fig. 2).

To model variation in development, we used time-varying distributed delays (Goudriaan 1973, Manetsch 1976). Briefly, Erlang probability distributions that incorporate the variation of the current and previous development times are produced for each life stage by subdividing each stage into a given number of substages that delay the integration flow within stages. The number of substages, k_i, within a stage i is directly related with the variance about development time (DT) based on the equation: $k_i = DT_i^2/\sigma_i^2$, where DT_i and σ_i^2 are the mean development time and variance reported for the state i. The transition rate between substages within the stage and the outflow to stage $i+1$ is given by k_i/DT_i (Fig. 2).

Studies that report development rates of grape mealybug are scarce as rearing colonies is difficult, but data for second and third nymphal instars and adults were taken from observations of a field sample fed on potato (Grimes and Cone 1985). However, development data on eggs, crawlers, and oviposition rates, are missing (Grimes and Cone 1985), and were estimated based on the obscure mealybug, *Pseudococcus viburni* (Signoret) feeding on Concord grape, *Vitis labrusca* (Silva et al. 2017); the grape mealybug and the obscure mealybug are sister species (Downie and Gullan 2004). We assumed no distinction between males and females for immature stages and used the longest reported development time. Although males are reported to have an additional immature stage, development for third and fourth instar were joined into one stage as the mean duration of both stages is equivalent to the third instar for females (Grimes and Cone 1985, Silva et al. 2017) (Table 1). The model was run in degree days, so development times, DD_i, for stages i, and reproduction period, RD, reported in days were converted to degree days by $DT_i = (T_{exp} - T_{min}) * DD_i$ and $RT = (T_{exp} - T_{min}) * RD$, respectively. T_{exp} is the temperature at which development was studied, and T_{min} is the lower temperature threshold for the grape mealybug, which was set to 10 °C (Geiger and Daane 2001). Variances were obtained in degree days by $\sigma_i^2 = \left[(T_{exp} - T_{min}) * SE_{Di} * \sqrt{n_i}\right]^2$, where SE_{Di} and n_i are the reported standard error and sample size for the stage i, respectively. We kept track of males and females from the adult stage on and assumed 50%:50% distribution between sexes and calculated fecundity (eggs laid per degree day) with the product between the number of females and Fec/RT, where Fec and

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RT are fecundity and reproduction period in degree days of the obscure mealybug and were set to 83.9 and 476.6, respectively (Silva et al. 2017). The simulation was initiated with 1,000 eggs from 0 to 2,500 degree days with an integration time step of 0.0625, and using the Euler integration method.

Data Analysis

Weekly capture counts were converted to proportions of total captures per location and pooled over 6 yr of sampling. We assumed 2 generations were present in the dataset (Geiger and Daane 2001) and that

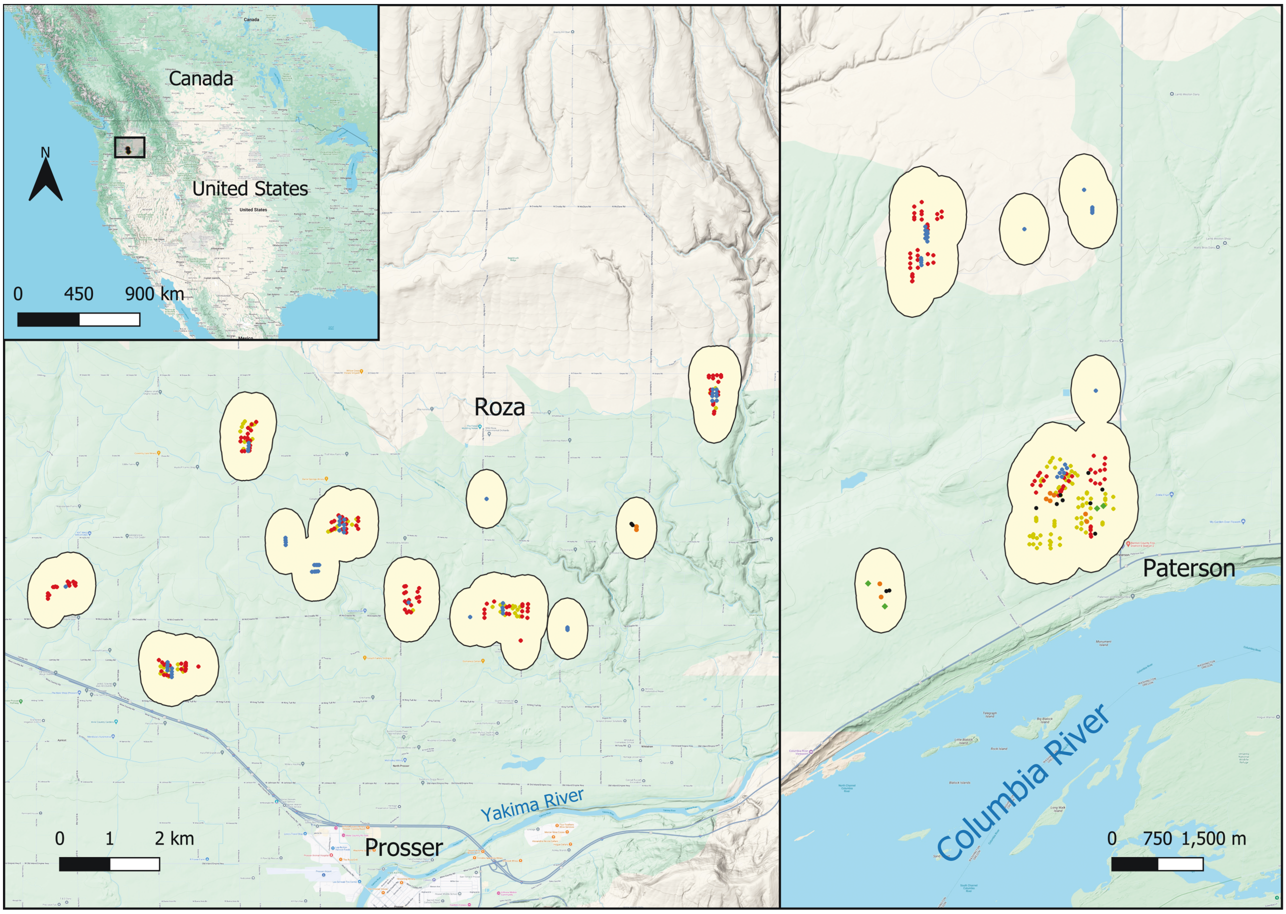

Fig. 1. Location of pheromone traps installed across a grape producing region in Paterson, Prosser and Roza, WA, USA. Dots represent 144 traps installed in 2009 (yellow), 195 in 2010 (red), 78 in 2011 (blue), 4 in 2021 (green), 10 in 2022 (orange), and 12 in 2023 (black).

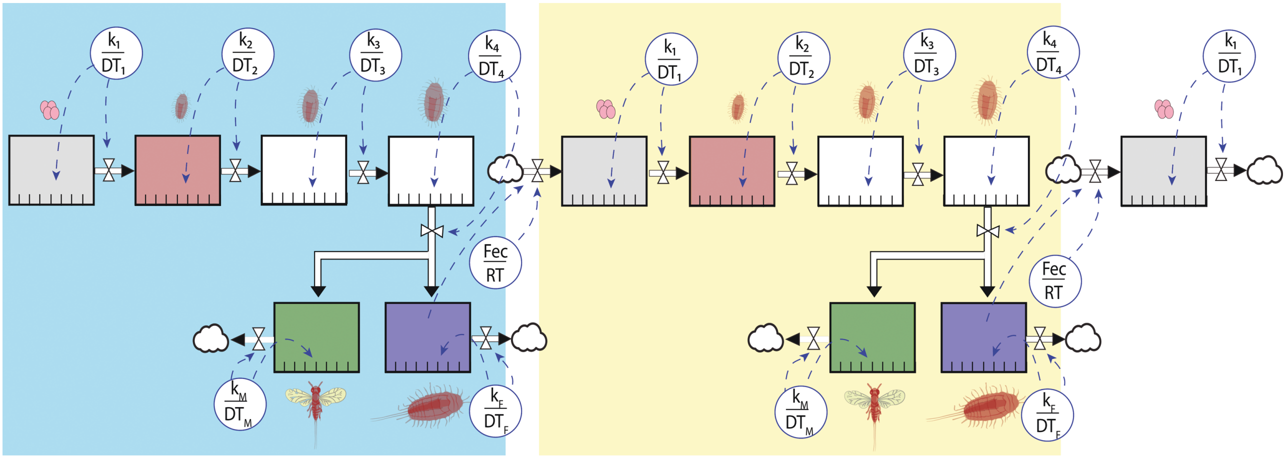

Fig. 2. Diagram of a phenology model for 2 generations (blue and yellow panels) and overwintering eggs (grey box to the right) of grape mealybug. State (life stages) and rate (development and fecundity) variables are indicated with boxes and blue circles, respectively. The flow between boxes is represented by white pipes, and clouds before and after the pipes represent new viable eggs laid and dead or overwintering individuals entering and leaving the system, respectively. Development rate is given by the quotient between k_i, the number of substages within a stage i, and development time DT_i, and eclosion rate is given by the quotient between Fec (fecundity) and RT (reproduction period in degree days). Stages 1, 2, 3, 4, M and F represent eggs, crawlers, stages 2 to 4 and adult males and females, respectively.

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Table 1. Development days, standard errors (SE), sample sizes (*n*), experimental temperatures, and references used to model grape mealybug. Development times in degree days and the number of substages, *k*, within each stage was calculated from the reported SE and *n*

Stage	Mean duration (days)	SE	*n*	Experimental temperature (°C)	Reference	Mean duration (degree days)	*k*
Egg	7.6	0.68	31	25	Silva et al. (2017)	114	4
Crawler[a]	14.29	0.26	392	25	Silva et al. (2017)	214.35	8
Second instar[a]	8.3	1.3	4	24.4	Grimes annnd Cone (1985)	119.52	10
Third instar[b]	12.2	2.6	11	24.4	Grimes and Cone (1985)	175.68	2
Adult female	34.6	8.4	10	24.4	Grimes and Cone (1985)	498.24	2
Adult male	1.4	0.8	7	24.4	Grimes and Cone (1985)	20.16	1

[a] No distinction between sexes was included for immature stages in the model and the highest development times between both sexes were used.
[b] Third and fourth instars for males were joint into one stage as the mean duration of both stages combined (12.2 degree days) is equivalent to the duration of the third instar for females (12.2).

the proportions of total captures across Julian and degree days are well described by gamma probability distributions. An expectation-maximization algorithm, which distinguishes mixtures of models in datasets based on the likelihood of frequency distributions, was used to determine the cut point between the 2 grape mealybug generations (Benaglia et al. 2009). The cut point between generations was established at the intersection between the gamma distributions estimated for each generation by the expectation-maximization algorithm. Parameters for gamma distributions across degree days and Julian days were estimated by maximum likelihood using the proportions constrained to the captures before and after the cut point between generations, respectively.

To determine the timing of grape mealybug phenology events, simulation model outputs were aligned with data from trap captures across degree days. We assumed that the maximum proportion of male captures per generation occurs when male abundance peaks, so we adjusted the degree days from the simulation model output by a 2-step process: (i) find the midpoint of the differences between the degree days with maximum abundance of males from the simulation model for each generation and the corresponding modes of the gamma distributions from the data, and (ii) subtract the midpoint of the differences between peaks of captures and simulated abundance from the degree days in the simulation model output.

All data analyses and model construction were carried out in R software version 4.2.3 (R Core Team 2024). The expectation-maximization function for the distinction between grape mealybug generations was conducted using the function gammamixEM in the mixtools package (Benaglia et al. 2009). Maximum likelihood estimation for the gamma probability distributions was performed with the mle2 function in the bbmle package (Bolker and Giné-Vázquez 2022).

Results

Of the 14,625 grape mealybug males captured in pheromone traps, 2,959 were captured in 2009, 4,352 in 2010, 2,145 in 2011, 1,770 in 2021, 1,555 in 2022, and 1,844 in 2023. We found 2 clusters of grape mealybug captures across Julian or degree days throughout the season, suggesting there are 2 generations per year in the key wine grape producing regions of Washington State. The expectation-maximization algorithm detected 2 mixed gamma components in the data, one for each adult mealybug generation that intercepted at 522.9 degree days. The gamma distribution parameters for the first and second generations across degree days were shape = 18.9 (SE = 0.76), rate = 0.062 (SE = 0.002); and shape = 39.7 (SE = 4.64), rate = 0.03 (SE = 0.004), respectively. And gamma parameters for captures across Julian days were shape = 120.7 (SE = 4.91), rate = 0.76 (SE = 0.03); and shape = 227.6 (SE = 27.3), rate = 0.99 (SE = 0.11) (Fig. 3).

Based on pheromone trap captures, the first seasonal adult population peak occurs at 286 degree days or 5 June, and the second at 1,112 degree days or 15 August, from the modes of the corresponding gamma distributions (Fig. 3). After aligning the timing of trap captures with simulation model outputs, simulated male population peaks occurred at 259 and 1,140 degree days for the first and second generation, respectively. In total, the peaks obtained from gamma distributions (male capture models) and the simulation model were 28 degree-days off, with peaks of male captures being slightly closer together (4%) than predicted by the model (Fig. 4C). Model output also mimicked the difference in shape for the first and second generation of males and predicted sessile second and third instar nymphs peak twice throughout the season, and that most first-generation eggs (99.9%) and crawlers (82.9%) hatch and develop before 1 January when degree accumulation begins (Fig 4A and B). Those predictions arose even when capture data was analyzed for each year individually. For example, male capture peaks in 2023 were registered the latest compared to other years (at 295.09 and 1,303.06 degree days for the first and second generation, respectively). Even if only the data collected in 2023 were used to align data with simulation model outputs, the model predicts that 98.6% and 52.7% of first-generation eggs and crawlers hatch and develop before 1 January, respectively.

Our model shows that optimization of insecticide applications to control grape mealybug crawlers is more feasible when treatments target the first generation. Hatching and development of second-generation crawlers spans over 1,000 degree days, which accounts for about twice the length of the hatching of first-generation crawlers, and would require a larger number of sprays to control (Fig. 4B). The simulation model output also suggests that most grape mealybug individuals must overwinter as single cohort of eggs, since outputs that include more than one overwintering stage (eg, eggs and crawlers) would result in wider, more mixed emergence curves that differ from the distinct clusters observed in the male capture data.

Discussion

Our study infers the best timing for insecticides for cryptic life stages of grape mealybug based on pheromone trap captures and phenology. We used probability distribution functions to model trap capture data across years and sites, and simulation modeling to calculate the timing of phenology. We then aligned trap captures and phenology to determine when crawler activity peaks in relation to the time when grape mealybug males are captured in traps. We found that most overwintering individuals should hatch and be

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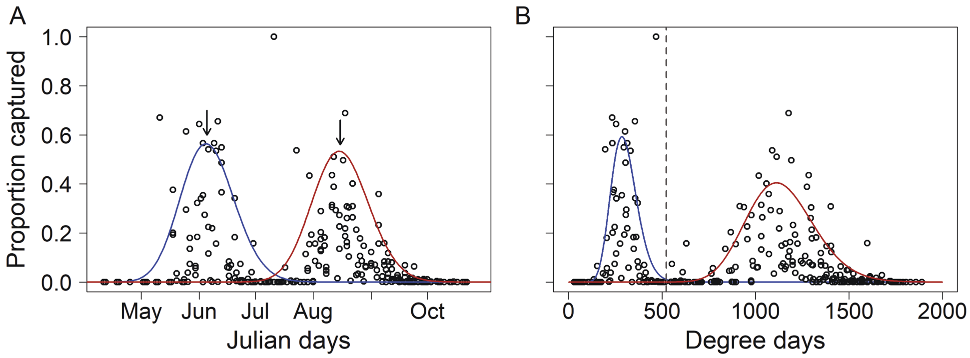

Fig. 3. Proportion of grape mealybug male captures in traps during the season between 2009 to 2011 and 2021 to 2023 in Paterson, Prosser, and Roza, WA, USA, across (A) Julian and (B) degree days. Blue and brown curves show gamma probability distribution functions fit to captures in the first and second generation, respectively. Arrows in (A) denote the 2 seasonal peaks of male captures occurring on 5 June and 15 August. The vertical line in (B) denotes the estimated cut point between generations at 523 degree days.

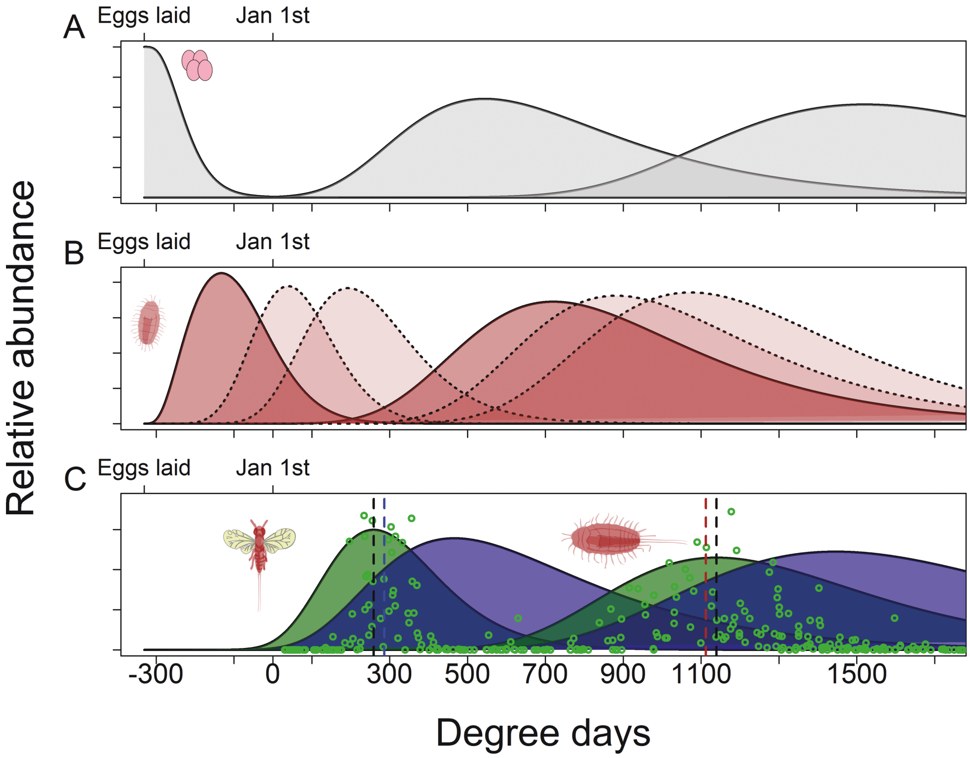

Fig. 4. Grape mealybug phenology model output for: A) eggs, B) nymphs, and C) adults across degree days. The output is aligned with the timing of male captures in traps by adjusting degree days of the simulations so that the peaks of captures (vertical blue and brown lines) and male abundance from model output (vertical black lines) are closer together for both generations. In (B), grape mealybug crawlers are shown in dark pink with solid curves, and second and third nymphal stages in pale pink with dashed curves. In (C), males are shown in green, females in blue, and green dots represent observed proportions of grape mealybug males in traps. Model outputs are shown in relative abundance of individuals as absolute quantities are context dependent.

active as crawlers before annual degree-day accumulation begins, and that sessile nymphs and adult males may peak twice at about the same time during the season. These results suggest that insecticide treatments made by the time the first male captures are detected, as suggested previously (Walton et al. 2013), may not efficiently control grape mealybug GLRaVs-infective crawlers from the overwintering generation.

Our dataset showed a consistent bimodal pattern of male captures in traps across Julian or degree days. This is in line with previous studies in the US Pacific Northwest that report grape mealybug males peak in June and August, except for the Willamette Valley (Oregon) where a single peak is observed (Grasswitz and James 2008, Bahder et al. 2013, Walton et al. 2013). Yet, Walton et al. (2013) observed male peaks occurred between 576 and 750 degree days for the first generation, and between 981 and 1,235 degree days for the second, differing from our findings of 286 and 1,112 degree days for the first and second peaks, respectively. The separation between peaks reported by Walton et al. (2013) is about half the separation found in this study (405 to 485 vs 826 degree days) and is hard to reconcile with our model, whose separation between male population peaks is about 880 degree days. These mismatches may be due to monthly sampling employed by Walton et al. (2013) compared with the weekly sampling of this study.

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It is difficult to compare the predictions of our model with field observations of grape mealybug life stages other than adult males. Sampling of crawlers and sessile forms of the grape mealybug is particularly hard, because they may inhabit different parts of vines, especially hidden, hardly reachable locations (Geiger and Daane 2001). For example, Walton et al. (2013) sampled vine plants between April and September sessile grape mealybug forms and found that most crawlers across the Columbia basin are found in May, before the first peak in pheromone trap captures. However, our predictions indicate that, by early May (about 100 to 200 degree days) (Fig. 3A), most individuals should be in second or third instar, followed by eggs, with relatively few crawlers (Fig. 4). Interestingly, our predicted population structure in early spring is more like what Walton et al. (2013) found in Southern Oregon. Walton et al. (2013) noticed that population dynamics of all sessile stages consistently follows a bimodal pattern that peaks in June and August like that shown by male captures in pheromone traps. Our simulation model predicts that second and third instar nymphs peak at about the same time as males for both generations (Fig. 4B and C), which may explain the observations reported by Walton et al. (2013).

Our approach has several major assumptions. First, parameters used to run the simulation phenology model were extracted from a combination of studies in different crops and with 2 mealybugs. Most development times and variances were extracted from a study of a small cohort of grape mealybug individuals in vineyards, but fed with potato sprouts once they were confined in the laboratory (Grimes and Cone 1985), which may have affected development and fecundity (Cocco et al. 2021). Parameters that could not be extracted from Grimes and Cone (1985) were obtained from a closely related species, the obscure mealybug. The distribution of both the grape mealybug and the obscure mealybug overlap in most grape-growing regions, although areas with only one mealybug species occur due to quarantine restrictions (Cocco et al. 2021). Although we assumed development rates of both species are similar, variation in this assumption could affect our model. Overall, we found that the separation between maximum grape mealybug male captures in pheromone traps and in our model differed by only 27 degree days (1 or 2 Julian days). This suggests our approach was effective at matching field trap data.

This study shows that the best time to apply controls for grape mealybug crawlers is about 80 to 150 degree days before the season begins. As temperatures above 10 °C are rare between November and February across the US Pacific Northwest, very few degree days are expected to accumulate off-season. Thus, those 80 to 150 last degree days, which are critical for egg hatching, crawler settling, and GLRaVs spread (O'Hearn and Walsh 2021), may occur in October, when vine plants start their winter cycle. This could be problematic since systemic insecticides may be less effective when plants' metabolic activity decreases and so does product uptake and insect intoxication by feeding. Systemic insecticides are widely used to reduce grape mealybug populations even if they do not confer protection against GLRaVs spread (O'Hearn and Walsh 2020), and applications occur primarily between April and June, regardless of counts in pheromone traps (Daane et al. 2006). This study shows that control strategies that do not rely on plant's metabolic activity should be applied by late autumn and that any treatments applied after the season begins are unlikely to be effective in reducing grape mealybug crawlers and GLRaVs spread. More broadly, our approach shows how linking phenology models with field data can be used to estimate key population parameters and guide insecticide treatments for a major pest.

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Author contributions

Stephen Onayemi (Conceptualization [equal], Investigation [equal], Methodology [equal], Writing—review & editing [equal]), Diego Rincon (Conceptualization [equal], Formal analysis [lead],Software [lead], Visualization [lead], Writing—original draft [lead], Writing—review & editing [equal]), Brian Bahder (Data curation [equal], Writing—review & editing [equal]), David Crowder (Conceptualization [equal], Funding acquisition [equal], Supervision [equal], Writing—review & editing [equal]), and Doug Walsh (Conceptualization [equal], Funding acquisition [lead], Supervision [equal], Writing—review & editing [equal])

Conflicts of interest. None declared.

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