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Modeling the relationship between insect phenology and field monitoring data with variable sampling efficacy

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ABSTRACT

Decision-support systems for pest management rely on phenology models to predict the timing of pest life cycles as well as monitoring populations through sampling. Phenology models are regularly used to predict biological events that are important for management, such as the presence of a certain life stage targeted by pesticides. However, while monitoring data are often intuitively used by producers to estimate pest pressure and make decisions, capture data are rarely linked with phenology models to generate pest forecasts. Here, we introduce a model that adjusts phenology predictions across degree-days based on the sampling efficacy of trapping networks. Specifically, we created a simulation model to account for the delay in observed trap captures with respect to predicted phenology as a function of sampling efficacy, measured as the probability of individuals being sampled per degree-day. Results from the simulation were used to derive a functional relationship between the shape of the phenology model and probability of capture per degree-day. The model was then tested using trapping data for codling moth, *Cydia pomonella*, from eight orchards in western USA and Canada. We found that the overall average error in predictions decreased by over 50% when forecasting curves were adjusted for site-specific sampling efficacy. These results suggest a key difference in the shape between phenology models and observed pest captures in the field can be described through cumulative binomial delays. More broadly, our study shows that pest forecasting and resulting management decisions might be refined by adjusting model predictions to site-specific sampling profiles.

1. Introduction

Integrated management strategies for insect pests often require robust phenology models that relate heat unit accumulation (i.e., degree-days) to predict the development of pest life stages, and reliable sampling networks to track the abundance and spatial distribution of pest populations (Damos, 2015). While phenology models indicate the rate at which pest populations are expected to develop, and when life stages targeted for management will be present, trap captures are used to intuitively gauge pest pressure and select a treatment program. A meaningful connection between phenology models and field data is therefore key to producing predictions that can be validated by data. However, field observations are highly dependent on sampling efficacy, and real-world pest observations often differ from the predictions of pest phenology models.

Pest management programs that integrate monitoring and weather data into models often produce risk assessments and inform timing of management actions (Damos, 2015; Jones et al., 2010). Such programs are widely used in temperate regions, including tree-fruit crop systems in Europe and the USA (Graf et al., 2002; Jones et al., 2010). For example, codling moth (*Cydia pomonella*) is a major tree fruit pest worldwide, and phenology models are used to assist in the design of insecticide treatment schedules. Many producers also invest heavily in pheromone traps to capture data on pest abundance in the field, allowing them to forecast future dynamics, estimate risk, and also gauge effectiveness of controls. However, these data are rarely linked with phenology models directly, even though such models may be inaccurate if they fail to account for sampling efficacy (Rincon et al., 2024). For example, even if a phenology model accurately predicts emergence of codling moth adults, growers may fail to capture adults for many

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reasons, particularly when the pest is at a relatively low abundance. Understanding how pest dynamics in the field relate to sampling efficacy could greatly improve predictions of phenology models.

Although the behavioral patterns of codling moths within pheromone trap networks have been studied (Adams et al., 2017), the connection between cumulative captures and progression of adult emergence across degree-days has received little attention. Understanding the functional relationship between sampling efficacy and phenology is key to fine tune within-season model predictions that can trigger insecticide treatments based on capture data. Yet, sampling efficacy is site-specific, as it is affected by trap density, which varies among orchards, and pheromone plume reach and attractiveness, which depend on local weather and bait age (Kershner, 2021; Turchin, 1998; Witzgall et al., 2008). In theory, a 'perfect' sampling network, which captures every adult moth the day it emerges, would exactly reflect the predicted proportion of emerged adults from the phenology model. However, population trajectories in real (imperfect) sampling networks are often delayed from trajectories predicted by phenology models. This is especially true at the start of the season when pest population sizes are too low to be detected, and at the end of each generation when moths are caught long after 100% emergence (Rincon et al., 2024).

Here, we introduce a model to describe the functional relationship between the cumulative proportion of adult emergence predicted by a codling moth phenology model and the cumulative proportion of males caught in a pheromone trap network. The relationship is based on sampling network efficacy, which was calculated as the binomial probability of individual males being captured per degree day. In practice, sampling efficacy can be determined from historical data from the network and then used to refine predictions by adjusting the shape of the phenology curve for subsequent years. The procedure was validated with male capture trajectories from seven orchard sites in western USA and Canada, allowing us to test whether incorporation of site-specific conditions into pest forecasting models can improve outputs and increase trust in evidence-based recommendations.

2. Methods

2.1. Model description

To describe the difference between the cumulative proportion of codling moth adults captured in pheromone traps and the cumulative emergence predicted by a phenology model, we built a discrete-time simulation model that progressed in degree days, *DD*. The system was restricted to the overwintering generation and made up of active adults, each with a constant probability of being captured, hereafter referred to as the net average sampling efficacy, *q*. The total number of moths across *DD* was calculated from the proportion of adult emergence, $f(DD)$, predicted by a phenology model developed by Jones and Wiman (2012):

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

where $z = \frac{DD-\xi}{\lambda}$, γ, and δ are shape parameters, λ is a dispersion parameter, and ξ a location parameter. Parameters γ, δ, λ, and ξ were set to 1.07, 1.24, 577, and 69.0, respectively, for the overwintering generation of emerging codling moth adults (Jones and Wiman, 2012).

Mortality was incorporated by keeping track of the average age since emergence of the active adult population, DD_{age}, and by removing the corresponding proportion of individuals for the age-specific survival rate, l_x, which is given by Jones and Wiman (2008):

$$l_x(DD_{age}) = \exp\left(\frac{A}{G}\left(1 - \exp\left(G \cdot DD_{age}\right)\right)\right) \quad (2)$$

where *A* is the initial mortality rate and *G* is the senescence rate, which were 0.0026 and 0.045, respectively.

The number of captured adults at *DD* degree days, C_{DD}, from a population A_{DD} is:

$$A_{DD+1} = \left[l_x(DD_{age}) + q\right] \cdot \left[A_{DD} + N * f(DD+1)\right] \quad (3)$$

$$C_{DD+1} = \cdot\left[A_{DD} + N * f(DD+1)\right] \cdot q$$

where *N* is the total adult population to be modeled for the season. The number of cumulative captures is the total number of adult codling moths taken out of the system by the *q* term, as for any reasonably large *N* the binomial process is adequately approximated by the mean. The capture trajectories, C_{DD}, thus become a version of the phenology model (Eq. (1), $f(DD+1)$) that includes age-specific survival (Eq. (2), $l_x(DD_{age})$), adjusted by the accumulative delay caused by a binomial capture process, and scaled vertically by adult population size.

2.2. Model calibration

Male capture trajectories, C_{DD}, were produced using a set of 800 values for *q* that were regularly spaced between 0.001 and 1. Non-linear least squares regression using the Levenberg–Marquardt algorithm (Levenberg, 1944) of the values for *q* was performed on three of the phenology model parameters (Eq. (1)): the shape parameters, γ and δ, and the dispersion parameter, λ, to determine the functional relationships between them. We excluded the location parameter, ξ, from this analysis because sampling efficacy is only expected to affect the shape and the length of the resulting curve, but not its location across the x-axis.

We used 4th order rational functions to find both γ and δ with *q* as the predictor, where γ was estimated as:

$$\hat{\gamma}(q) = \frac{a_{\gamma4}q^4 + a_{\gamma3}q^3 + a_{\gamma2}q^2 + a_{\gamma1}q + a_{\gamma0}}{b_{\gamma4}q^4 + b_{\gamma3}q^3 + b_{\gamma2}q^2 + b_{\gamma1}q + 1} \quad (4a)$$

and δ was:

$$\hat{\delta}(q) = \frac{a_{\delta4}q^4 + a_{\delta3}q^3 + a_{\delta2}q^2 + a_{\delta1}q + a_{\delta0}}{b_{\delta4}q^4 + b_{\delta3}q^3 + b_{\delta2}q^2 + b_{\delta1}q + 1} \quad (4b)$$

where $a_{\gamma4},\ldots a_{\gamma0}$ and $b_{\gamma4},\ldots b_{\gamma1}$, and $a_{\delta4},\ldots a_{\delta0}$ and $b_{\delta4},\ldots b_{\delta1}$ are regression coefficients. The function used to describe λ as a function of *q* was a power law with an added 'bump' and a limit, which is defined as:

$$\hat{\lambda}(q) = c_{\lambda0}q^{c_{\lambda1}} + \frac{c_{\lambda2}}{4c_{\lambda4}}\operatorname{sech}\left(\frac{q - c_{\lambda3}}{2c_{\lambda4}}\right) + 577.2 \quad (4c)$$

where $c_{\lambda4},\ldots c_{\lambda0}$ are regression coefficients and 577.2 is the limit, which equals λ in Eq. (1). The limit is set to 577.2° days because that is when emergence of the overwintering codling moth adults is completed (Jones and Wiman, 2012). The use of the hyperbolic secant to introduce a bump into the power law was not chosen for biological significance, but because it resulted in a lower regression error than other similarly shaped functions during testing. The functional relationships between parameters $\hat{\gamma}$, $\hat{\delta}$ and $\hat{\lambda}$ and net average sampling efficacy, q, as described by Eq. (4a)-c after calibration, are shown in Fig. 2A-C.

2.3. Model evaluation and analysis

The model was validated on a pheromone trap dataset with weekly records from eight orchard sites in central Washington State, USA and Southern British Columbia, Canada. All sites included several contiguous orchards, one with records from 1995 to 2015 (excluding 2003), and the other seven sites from 2018 to 2021, for a total of 48 population trajectories (orchard-year combinations) (Fig. 1). All traps were wing traps or delta traps baited with 1 mg of the sex pheromone, (E,E)−8, 10-dodecadien-1-ol (codlemone), or with CM-DA Combo™ lures (3 mg

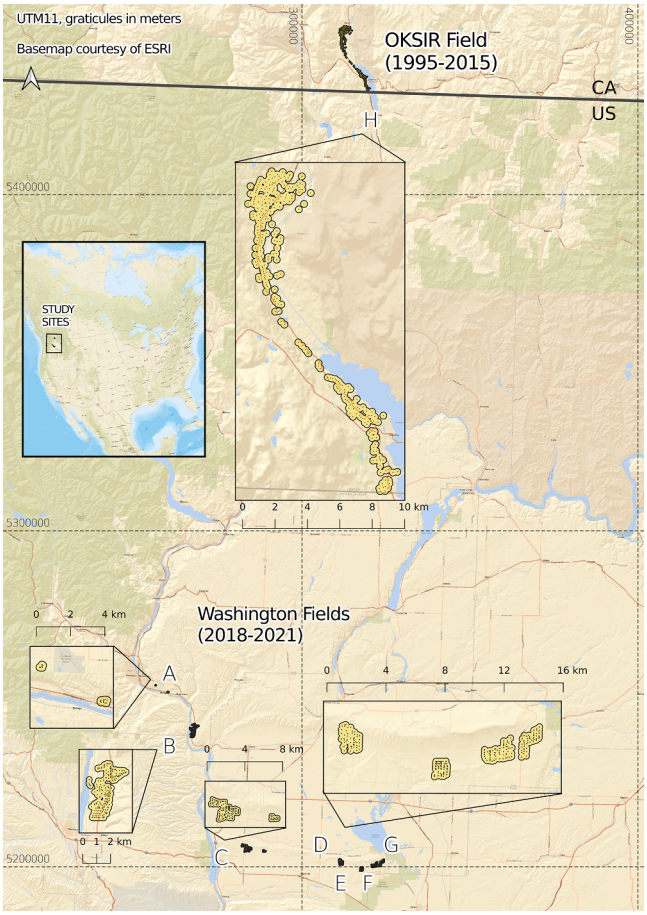

Fig. 1. Spatial overview of study sites with data collection time range annotations and magnified views of study sites displaying trap locations as well 260-m effective trap coverage areas. The center-left frame highlights the position of the study sites in relation to the rest of North America.

codlemone with 3 mg pear ester), when mating disruption was used (Trécé Inc., Adair, OK, USA). Effective trap densities for each site were determined from the joint area of all traps with a 260-m buffer, the capture radius of such pheromone traps (Adams et al., 2017), and ranged from 0.08 to 0.57 traps per ha. It should be noted that our estimates of the effective trap densities may differ from growers' assessments, which are typically based on traps per area of cultivated land. This was necessary for our analysis because adjacent trap networks may interact with each other, even if they belong to different orchards, and reliable yearly data on total area of cultivated land at each study site is not available.

Our approach was tested by obtaining values of q for each site-year to first assess the effect of considering site-specific q estimates on prediction accuracy, and second to assess consistency of q across trap densities. Prediction accuracy was assessed by applying the approach of Rincon et al. (2024) to produce short-term predictions of future trap captures based on prior captures and predicted adult emergence from a phenology model. This approach assumes cumulative captures and emergence are proportional, so cumulative captures per trap at any future DD is given by:

$$\sum_{1}^{j} \hat{x}(DD_j) = \frac{\sum_{1}^{i} x(DD_i) \times \int f(DD)}{\int f(DD_i)} \tag{5}$$

where $\sum_1^j \hat{x}(DD_j)$ and $\sum_1^i x(DD_i)$ denote cumulative captures per trap at any future DD and at a present DD_i, respectively, and $f(\cdot)$ is the phenology model for codling emergence for the overwintering generation (Eq. (1)). The site-specific values for q were estimated yearly from moth capture data from previous years at each site. Values for q were obtained by least-squares optimization of the phenology model with calibrated functions of $\hat{\gamma}(q)$, $\hat{\delta}(q)$, and $\hat{\lambda}(q)$ replacing parameters γ, δ, and λ, and parameter ξ fixed at its original value of 69.0 as:

$$\frac{x(DD)}{\sum x} = \frac{\hat{\delta}(q)\cdot\exp\left(-\frac{1}{2}\left(\gamma + \hat{\delta}(q)\ln\frac{z}{1-z}\right)^2\right)}{\hat{\lambda}(q)\cdot\sqrt{2\pi}\cdot z\cdot(1-z)} \tag{6}$$

where $z = \frac{DD - 69}{\hat{\lambda}(q)}$ and $\frac{x(DD)}{\sum x}$ are proportions of moth captures across degree days for the overwintering generation from all previous years.

With model parameters calibrated for each site, predictions were produced at $DD_i = 300$ for the rest of the overwintering generation (577° days) with and without the sampling efficacy adjustment for all years. Predictions were then compared with the 48 trajectories, and the mean absolute error (MAE) was used to compare model performance (Hyndman and Koehler, 2006). It is given by:

$$MAE = \frac{\sum_{\{i=1\}}^{n} |e_i|}{n} \tag{7}$$

where e_i is the residual for sample i, or the difference between the data and the model prediction, and n is the number of samples. The values of MAE obtained with the adjusted and unadjusted models were examined as a function of cumulative captures for each site and year in a log scale.

To examine the consistency of q across trap densities, values of q were obtained for each site-year combination, excluding those below 2.5 cumulative captures per trap, where sampling error dominates the data. Estimation of q values was conducted as described earlier, except that the location parameter ξ was estimated for each site from capture data of all years using the maximum likelihood estimator under the assumption of normally distributed residuals (Hodson, 2022). Estimates of ξ for each site were then fixed for each year, prior calculation of q. By making ξ vary across sites, we aimed to control for site-specific codling moth pressure and for changes in emergence patterns across different latitudes (Jones et al., 2013) to obtain more precise estimates for q. The relationship between estimated capture efficacy, q, and trap density in each site-year combination was examined with a rational function of the form:

$$q = \frac{a_{q1} T^2}{b_{q2} T^2 + b_{q1} T + 1} \tag{8}$$

where T is the estimated trap density per ha at each site, and a_{q1}, b_{q1} and b_{q2} are regression coefficients. Parameter estimation was performed by non-linear least squares.

3. Results

Parameter estimates for rational functions (Eq. (4a), 4b, and 4c) that describe shape and dispersion parameters of the phenology model for emergence of overwintering codling moth adults (Eq. (1)) are shown in Table 1. Using these equations, we simultaneously calibrated γ, δ, and λ according to q, a parameter associated with trap capture efficacy per site (Fig. 2). After obtaining values for q from data collected from prior years, the overall average error in predictions decreased by over 50%. For the unadjusted model that did not recalibrate the shape and dispersion parameters based on capture efficacy, the average error was 21% and ranged from 3.2% to 41%, while the average error for the model adjusted for sampling efficacy was 8.0% and ranged from 1.8% to 20%. The relationship between average cumulative captures per trap and mean absolute error was positive for the unadjusted version of the phenology model [intercept = −2.37 (SE = 0.18), slope = 0.26 (SE = 0.094), $p = 0.012$], and negative for the phenology model adjusted for the sampling efficacy [intercept = −2.73 (SE = 0.21), slope = −0.17 (SE

Table 1
Parameter estimates for rational functions to describe shape and dispersion parameters of a JohnsonSB probability distribution function that predicts the emergence of overwintering codling moth adults. Numbers in parentheses are standard errors.

Coefficients					
Shape parameter γ (Eq. (4a))	$a_{\gamma 4}$	$a_{\gamma 3}$	$a_{\gamma 2}$	$a_{\gamma 1}$	$a_{\gamma 0}$
	1.26×10^8	7.36×10^5	13,332	335.0	1.70
	(3.44×10^6)	(1.31×10^5)	(1088.2)	(8.12)	(0.00321)
	$b_{\gamma 4}$	$b_{\gamma 3}$	$b_{\gamma 2}$	$b_{\gamma 1}$	
	1.20×10^8	-9.24×10^5	65,919.6	−317.1	
	(2.96×10^6)	(1.09×10^5)	(6666.4)	(2.16)	
Shape parameter δ (Eq. (4b))	$a_{\delta 4}$	$a_{\delta 3}$	$a_{\delta 2}$	$a_{\delta 1}$	$a_{\delta 0}$
	2.02×10^8	7.74×10^6	-3.45×10^4	4.38	0.713
	(1.68×10^6)	(1.77×10^5)	(1.30×10^3)	(4.69)	(0.0012)
	$b_{\delta 4}$	$b_{\delta 3}$	$b_{\delta 2}$	$b_{\delta 1}$	
	1.69×10^8	4.32×10^6	−1403.0	644.3	
	(1.35×10^6)	(1.26×10^5)	(949.4)	(3.09)	
Dispersion parameter λ (Eq. (4c))	$c_{\lambda 4}$	$c_{\lambda 3}$	$c_{\lambda 2}$	$c_{\lambda 1}$	$c_{\lambda 0}$
	0.0011	0.0022	35.1	1.15	2.266
	(3.41×10^{-6})	(5.00×10^{-6})	(0.142)	(0.002)	(0.0079)

$= 0.11$), $p = 0.11$] (Fig. 3).

The mean capture efficacy, q, across all site-year combinations was 0.027 and ranged from 0.005 to 0.068. Effective trap density averaged 0.32 traps per ha and ranged between 0.08 and 0.58, with most of the low-density site-year combinations located in southern British Columbia (Fig. 1). We found that the relationship between q and the corresponding trap densities was non-linear and described well by a rational function (Eq. (8)) with parameters $a_{p1} = 0.41$ (SE = 0.19), $b_{p1} = -1.67$ (SE = 0.98) and $b_{p2} = 75.2$ (SE = 8.01). Capture efficacy peaked at 0.12 effective traps per ha and remained relatively constant below $q = 0.02$ for densities > 0.25 traps per ha.

4. Discussion

Our findings suggest that the difference in shape and dispersion between phenology models and capture trajectories can effectively be accounted for in population forecasts by introducing estimates of sampling efficacy. Although the functions that describe the shape and dispersion parameters of the codling moth phenology model lack biological meaning and are aimed to provide empirical approximations, our approach provides a mechanistic link between phenology and apparent population dynamics. Incorporating sampling efficacy into forecasts might thus improve accuracy of phenology-based forecasting models based on site-specific trap networks. Our approach is also useful to determine measures of capture efficacy for specific sites, which is key to monitoring performance of pheromone trap networks over time.

The phenology-based estimation of trap networks' sampling efficacy we propose here can be easily implemented in systems that assist pest population forecasts with phenology models. In the case of the codling moth, implementation only requires historical data for a given trap network, which can be used to find parameter q, by least-squares optimization of Eq. (6). The larger the historical dataset, the more precise is the estimate for q. Once q is known, Eq. (4a)-c are then used to obtain adjusted parameter values for a phenology model that is site-specific and produces forecasts of the distribution of capture data for subsequent years. This forecast of the distribution can be combined with a hypothesis testing framework, such as the Sequential Test of Bayesian Posterior Probabilities (Rincon et al., 2025), to predict the likelihood of pest captures exceeding an economic threshold after a set amount of degree day accumulation given early-season data. This unlocks the possibility of statistically-backed, site-specific decision making based on existing trapping networks for a variety of agricultural pests during critical management timings, reducing both the cost and environmental impact of cautious over-management.

The mechanistic link between phenology and field data should allow for a more meaningful interpretation of data from trap networks. While there are no established economic thresholds for codling moth, due to the lack of clear links between trap captures and pest abundance (Adams et al., 2017), most extension programs recommend use of pheromone capture data only to gauge pest activity because capture numbers can poorly indicate a need for controls. As an alternative, producers typically develop experience-based, trap network-specific thresholds for controls based on cumulative pheromone trap captures (Adams et al., 2017; Riedl and Croft, 1974). Approaches that produce in-season predictions of future trajectories based on phenology models and data collected early in the season have been proposed to help plan for appropriate treatment programs (Rincon et al., 2024). This study shows that estimates of sampling efficacy can be used to further improve the link between population dynamics and phenology, and that site-specific information can be leveraged to reduce error in predictions derived from phenology models.

In addition to the improvements made from adjusting phenology models based on real-world sampling data, there are multiple applications stemming from the results relating to the measurement of absolute trap efficacies. Most comparisons of trapping efficacies use mean moths captured per trap or mean moths captured per time unit (e.g., Adams et al., 1989; Joshi et al., 2011; Mitchell et al., 2008). These methods are dependent on population size and therefore are only applicable for comparisons across the same site-year combinations. Other approaches use mark-recapture techniques to determine the proportion of recaptured moths from different release distances, but these studies are labor and resource intensive (Adams et al., 2017; Curtiss et al., 2023). Our capture efficacy metric, probability of moths being caught per degree day, is independent of population size, and can be measured without a dedicated experimental design.

Our results on the relationship between trap density and trapping efficacy also provide evidence for the existence of an optimal density past which effects such as sensory fatigue and competitive attraction reduce the chance for moths to be captured (Witzgall et al., 2008). However, the optimal effective trap density we calculated (0.12 traps/ha) should not be directly applied as a recommendation, as our density calculation method differs greatly from the methods used by orchard managers in practice. Furthermore, our study is focused on information gains from trap networks and does not imply that our estimates of q can be directly associated with mass trapping efficacy under field conditions. This can instead be taken as evidence that more traps per unit area do not necessarily result in more statistically usable information. Particularly, the Washington orchards examined here used a trapping density many times greater than typical but did not achieve any measurable gains in information. Rather than providing these results as a prescription of an optimal trapping density, they should instead serve as a warning against over-investing in higher than average trapping densities when the goal is to inform management.

One limitation of the accumulating binomial delay model is that it assumes a uniform capture efficacy across the entire sampling period. Yet, many field-collected trajectories that do not follow the shape of Johnson-SB curves are the result of transient effects, such as rain, wind or temperature, which impact capture rates of codling moth in pheromone traps (Batiste et al., 1973; Pitcairn et al., 1990; Witzgall et al., 2008). Furthermore, making changes to the structure or design of the sampling network, through adding or removing traps, or changing pheromone compounds, or trap structures, will have effects on sampling efficacy. Thus, when changes of such nature occur, new estimations of sampling efficacy should be conducted, ideally through multiple

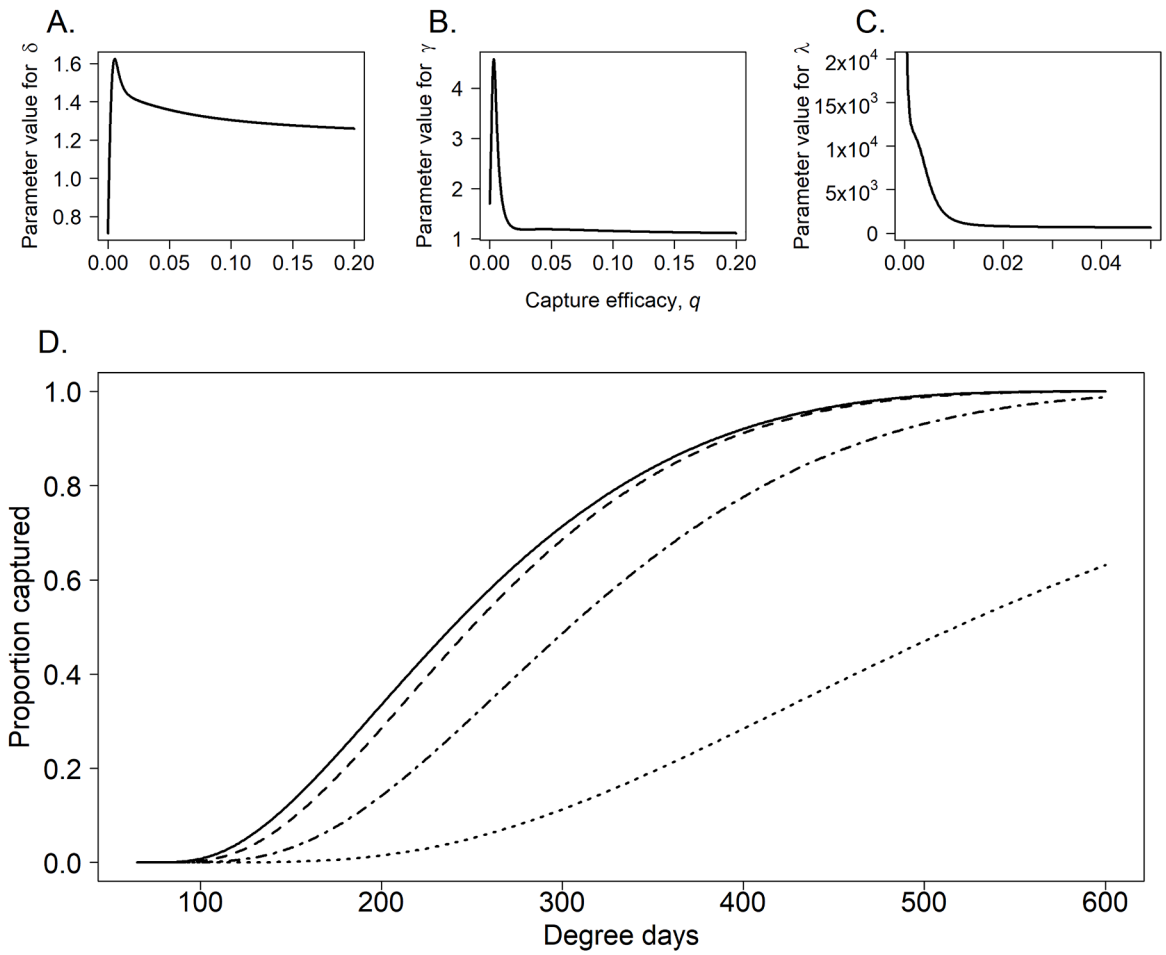

Fig. 2. Functional relationship between pheromone trap efficacy, q, and a phenology model that describes cumulative emergence of the adult codling moth overwintering generation (Eq. (1)). Empirical descriptions of shape and dispersion parameters δ, γ, and λ as a function of q are shown in A, B and C, respectively. The effect of various levels of capture efficacy on the phenology model are shown in C, where the solid curve represents the unadjusted phenology model ($q = 1$), the dashed curve is the model for $q = 0.08$, the dot-dashed for $q = 0.02$, and the dotted for $q = 0.008$.

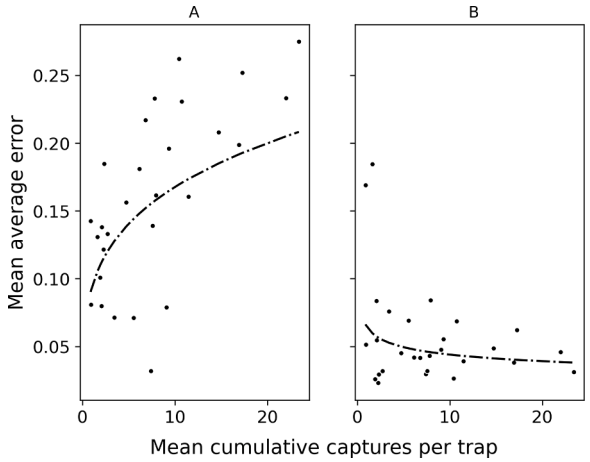

Fig. 3. Mean absolute error as a function of average codling moth cumulative captures per trap of predictions produced with a phenology model (A), and a version adjusted for the sampling efficacy of the corresponding trap network (B). The dashed-dotted curve is the overall trend represented by a power law model.

seasons, before forecasting accuracy can be entirely recovered.

Our study shows that there is opportunity to refine pest forecasting by adjusting models to site-specific sampling profiles. Further work should test decision making procedures using these site-specific sampling profiles for accuracy, and tailoring them over time to increase effectiveness. Our approach might be facilitated by integration of the site-specific forecasting tools into a web-based decision aid system for real world testing, which would also provide opportunities to develop new trap-density recommendations. This methodology could also be applied to model generations of moths other than the overwintering generation, which would extend usefulness of the recommendations. More broadly, optimizing parameters for models based on trap capture efficacy could be leveraged to investigate regional differences in emergence times that account for differences in capture efficacy. Producers might also be able to better understand how abiotic factors such as wind or rain, as compared to biotic factors such as population size, affect trap captures. Overall, further incorporation of real-world trap data into predictions of phenology models will improve forecasts and pest management outcomes.

CRediT authorship contribution statement

Izzy L. McCabe: Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Diego F. Rincon:** Writing – review & editing, Methodology, Data curation, Conceptualization. **David W. Crowder:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare they have no competing financial interests or personal relationships.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2026.111737.

Data availability

All data and reproduction steps are available at the DOI link provided, as well as the GitHub repository it is sourced from PacificBird/InsectPhenologyCaptureSim (Original data) (Zenodo)

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