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Research

A Phenology Model for Simulating *Oobius agrili* (Hymenoptera: Encyrtidae) Seasonal Voltinism and Synchrony With Emerald Ash Borer Oviposition

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Abstract

In North America, the emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), continues to spread, and its egg parasitoid, *Oobius agrili* Zhang and Huang (Hymenoptera: Encyrtidae), is being released for emerald ash borer biocontrol well beyond their endemic climatic ranges in China. We developed a multiple cohort rate summation model to simulate *O. agrili* F_0, F_1, and F_2 generations, and emerald ash borer oviposition for examining host–parasitoid synchrony across a north–south gradient from Duluth, MN (latitude 46.8369, longitude –92.1833) to Shreveport, LA (latitude 32.4469, longitude –93.8242). Temporal occurrences of critical day length for *O. agrili* diapause induction were integrated into the model. We used *O. agrili* and emerald ash borer trapping data from south central and northwestern Lower Michigan for model validation. Simulations demonstrated that 1) F_0 adult emergence consistently occurred 2–5 d before emerald ash borer oviposition began; 2) F_1 adult emergence was most synchronized with peak emerald ash borer oviposition compared with other generations; and 3) emerald ash borer oviposition was complete, or near so, when F_2 adult emergence was predicted across the north–south gradient. Comparison of *O. agrili* trap captures with model simulations demonstrated that primarily two adult *O. agrili* generations (F_0 and F_1) emerged per year in Michigan and almost all F_2 larvae entered diapause despite day lengths longer than critical day length in south central Michigan. Critical day length varied temporally across the north–south gradient during emergence of *O. agrili* generations. Determining day lengths perceived by *O. agrili* larvae in the field should improve model realism for examining spatiotemporal variation in *O. agrili* population dynamics.

Key words: biological control, invasive species, rate summation model, host-parasitoid synchrony

Oobius agrili Zhang and Huang (Hymenoptera: Encyrtidae) is an egg parasitoid introduced into North America as part of a classical biological control program for emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) (Bauer et al. 2015). Emerald ash borer is an invasive pest of ash trees and threatens to functionally extirpate many North American ash species (Herms and McCullough 2014). Both emerald ash borer and *O. agrili* are native to China, with *O. agrili* more or less restricted to northeastern China (Liu et al. 2007; Wang et al. 2015; Yao et al. 2016), and emerald ash borer having a considerably broader geographic distribution (Haack et al. 2002, Bray et al. 2011, Chamorro et al. 2015).

Since the discovery of emerald ash borer in Michigan and Ontario, Canada, in 2002 (Haack et al. 2002), it has spread south to Texas, north to Manitoba, Canada, east to Nova Scotia, Canada, and west to Colorado. Emerald ash borer has been detected in all eastern U.S. states except for Mississippi and Florida and all eastern Canadian provinces except for Newfoundland and Prince Edward Island (Emerald Ash Borer Information Network 2020). *Oobius agrili*, a solitary, parthenogenetic egg parasitoid, was approved for release in the United Startes in 2007 and in Canada in 2013 (Bauer et al. 2015, Duan et al. 2018). Since then, *O. agrili* has been released throughout much of emerald ash borer's distribution in North America and has been recovered at release sites in 14 U.S. states and 2 Canadian provinces (MapBioControl 2020). However, it is not known how well *O. agrili* will perform as an emerald ash borer biocontrol agent in climates that differ from those in its native distribution.

Oobius agrili is a multivoltine species that overwinters as mature diapausing larvae within host eggs. In its endemic range, *O. agrili* has at least two generations per year (Liu et al. 2007);

however, the number of generations that occur throughout its distribution in North America has not been determined. In the laboratory, *O. agrili* is capable of producing multiple consecutive generations that do not require diapause when reared under a 16:8 (L:D) h photoperiod (Yao et al. 2016). Diapause of *O. agrili* is induced when developing *O. agrili* larvae, within emerald ash borer eggs, are subjected to shorter day lengths (<14.25 h; Hoban et al. 2016, Larson and Duan 2016, Petrice et al. 2019). In addition, *O. agrili* adults can be separated into two distinct phenotypes based on their diapause history, which consequently determines their progeny's diapause response to photoperiod. These phenotypes are as follows: 1) adults that developed from diapausing larvae (diapaused adults) and 2) adults that developed from nondiapaused larvae (nondiapaused adults) (Hoban et al. 2016, Petrice et al. 2019). All progeny produced by diapaused adults develop directly to adult wasps and emerge when reared at day lengths ≥ 14.5 h, and a small percentage (ca. 10–20%) enter diapause when reared at day lengths < 14 h. In contrast, ca. 10% of progeny from nondiapaused adults will enter diapause when reared at day lengths ≥ 14.5 h, and 100% enter diapause when reared at day lengths < 14 h. The critical day length for diapause induction, when 50% of individuals enter diapause, is between 14.25 and 14.5 h of daylight (Petrice et al. 2019).

Emerald ash borer is primarily univoltine but may require 2 yr to complete development when emerald ash borer larvae develop in cooler climates, or are subjected to relatively high levels of host resistance (Cappaert et al. 2005, Wei et al. 2007, Wang et al. 2010). Emerald ash borer overwinters as mature larvae folded in a J-shape within pupation chambers in the outer-bark or outer-sapwood, or as immature larvae within feeding galleries in the cambial region of trees (Cappaert et al. 2005, Duan et al. 2010, Chamorro et al. 2015). Overwintered immature larvae continue feeding the following spring and summer, and after they are mature, create pupal cells where they overwinter as J-larvae. Mature emerald ash borer larvae must experience a chill period before they pupate and develop to adults (Duan et al. 2013). Adults emerge in spring or summer and feed on host foliage for several days before they become sexually mature and continue to feed on host foliage throughout their life. Oviposition begins after emerald ash borer females are sexually mature and have mated, and females can oviposit for several weeks in the laboratory (Rutledge and Keena 2012). Emerald ash borer phenology appears to be regulated predominately by temperature, with the exception of feeding larvae, which may also be influenced by levels of host–plant resistance (Cappaert et al. 2005).

Temperature plays a significant role on the population dynamics and temporal synchrony of emerald ash borer and *O. agrili* (Duan et al. 2014, Wetherington et al. 2017). For instance, *O. agrili* emergence from diapause and development of subsequent generations, which are thermally regulated, must be synchronized to emerge during emerald ash borer oviposition. However, it is not clear how the interaction of photoperiod and temperature affects *O. agrili* voltinism and diapause. Ideally, *O. agrili* diapause induction should be synchronized with the termination of emerald ash borer oviposition to prevent *O. agrili* adults from emerging after emerald ash borer oviposition has ended. Therefore, determining how the interaction of temperature and photoperiod affects the temporal synchrony of *O. agrili* with emerald ash borer oviposition is important for understanding their population dynamics (Wetherington et al. 2017, Petrice et al. 2019).

Degree-day models are commonly used for estimating the effects of temperature on insect development rates by correlating the development time of ectothermic organisms with the number of degree days that have accumulated. Degree days are calculated as the accumulated daily sums of the number of degrees the mean daily temperature is above a predetermined threshold. Brown-Rytlewski and Wilson (2004) developed a degree-day model for emerald ash borer emergence that is commonly used for making predictions of emerald ash borer adult emergence. More recently, Duarte (2013) developed a probit model based on degree-day accumulation to predict emerald ash borer emergence. Currently, there is no model (degree day or otherwise) to predict emerald ash borer sexual maturation, oviposition, or *O. agrili* phenology.

The simplicity of degree-day models makes them convenient for forecasting discrete phenological events of insects; however, their assumption that development rates are linear functions of temperatures can compromise their accuracy (Wagner et al. 1984, 1991; Gray 2012). Damos and Savopoulou-Soultani (2012) cited numerous studies that demonstrated insect development rates near their upper and lower developmental thresholds were nonlinear. Another approach to insect phenology modeling is to determine the development rates of insects at a range of temperatures including those near their upper and lower developmental thresholds. Nonlinear functions can then be fitted to rates and used to calculate the accumulated development over time as a function of temperature. This method is often referred to as 'rate summation' (Gray 2012, Régnière et al. 2012).

Realism of phenology models can also be improved by quantifying the variability of development rates within insect populations (Régnière 1984, Wagner et al. 1984). Depending on the genetic diversity within a population and interactions with environmental factors, there can be considerable variation in development rates among individuals within populations. A cumulative probability function is frequently used to describe this variability (Wagner et al. 1984). Developmental variability can be integrated into phenology models allowing independent cohorts to be tracked as they pass through subsequent life stages, giving more realistic estimates of the populations' response to temperature (Régnière 1984, Gray 2012).

The objectives of this study were to evaluate the temporal synchrony of *O. agrili* adult emergence with emerald ash borer oviposition and its interaction with *O. agrili* photoperiod-induced diapause across their geographic distributions in North America. We developed a temperature-driven multiple cohort rate summation model to simulate temporal synchrony of *O. agrili* with emerald ash borer oviposition. The accuracy of the model was assessed by comparing model simulations with emerald ash borer- and *O. agrili*-trap captures at four field sites sampled over a 3-yr period in Michigan. Model simulations were used to compare synchrony of *O. agrili* generations with emerald ash borer oviposition and the temporal occurrence of critical day length for *O. agrili* diapause induction at different geographic locations in the United States.

Materials and Methods

Temperature Assays for Determining Development Times

Development Time for *O. agrili* and Emerald Ash Borer Adult Emergence

We determined the development rate of *O. agrili* F_0 individuals (diapaused generation) from the diapausing larval stage to emerged adult, and of the F_1 and F_2 (first- and second-nondiapaused generations, respectively) from parasitoid egg to emerged adult. *Oobius agrili* used in this study originated from emerald ash borer eggs collected in Changchun, Jilin Province, China (43.8666 latitude,

125.3500 longitude) and were maintained for 36 generations in the USDA Forest Service Northern Research Laboratory (Michigan State University, East Lansing, MI). Diapausing F_0 *O. agrili* larvae were progeny of nondiapaused females. We forced these larvae into diapause by holding them in a short-day photoperiod (8:16 [L:D]) at 25°C immediately after parasitoid oviposition. After 30 d in short-day photoperiod, we transferred F_0 *O. agrili* larvae to 10°C for 30 d, then moved them to 4°C for 7–9 mo (chill period). After F_0 larvae had undergone chill periods, we reared individuals at 10, 15, 20, 25, 30, 34, or 39°C constant temperatures and monitored for adult emergence daily. Temperature treatments were repeated two to three times with different F_0 cohorts (Table 1). Individuals held in the 10°C treatment were transferred to 25°C after 60 d to allow development to be completed. This allowed us to measure the amount of development that occurred at 10°C, while reducing mortality of individuals held for extended periods at lower temperatures and minimizing the time required to conduct this temperature assay (Régnière et al. 2012). We calculated the development rate at 10°C using the following equation from Gray (2009):

$$ {}_iR_T(t) = [1 - ({}_it_{25}/{}_it_{c25})]/t_T \quad (1) $$

where ${}_it_{25}$ is the median time in days that individuals from the *i*th replicate were held at 25°C, ${}_it_{c25}$ is the median time required for individuals held at 25°C to develop and emerge as adults for the *i*th replicate (determined from the 25°C temperature treatment); t_T is the time in days that individuals for the *i*th replicate were held at the treatment temperature T (i.e., 10°C); and ${}_iR_T(t)$ is the development rate for the *i*th replicate.

We determined the developmental rates of the F_1 *O. agrili* generation by holding emerald ash borer eggs parasitized by F_0 adults at 10, 15, 20, 25, 30, 34, or 39°C constant temperatures and monitoring adult emergence daily. We obtained parasitized eggs by directly observing emerald ash borer egg parasitism by F_0 *O. agrili* adults in Petri dishes. Within 3 h of parasitism, emerald ash borer eggs were placed in one of the temperature treatments. Individuals held in 10°C were transferred to 25°C after 60 d for development to be completed. As with F_0 development, we calculated rates for transferred F_1 individuals using equation 1 and the median development time for the F_1 25°C-constant-temperature treatment representing the variable ${}_it_{c25}$. Each temperature treatment was repeated one to three times using different F_1 cohorts (Table 1). We assumed that developmental rates for the F_2 *O. agrili* generation were the same as the F_1 generation (personal observation).

We determined emerald ash borer adult female emergence rates by rearing emerald ash borer adults from white (*Fraxinus americana* L.) and green ash (*F. pennsylvanica* Marshall) logs that contained diapausing J-larvae. Logs were cut from naturally infested ash trees during the month of January at Doake Research Forest, Winfield, IN (41.368855 latitude, −87.253270 longitude) in 2016; West Lafayette, IN (40.504359, −86.901039), Okemos, MI (42.693989, −84.382596), and Ithaca, MI (43.233431, −84.446431) in 2017; and West Lafayette, IN, in 2018. Logs were stored at 4°C for a maximum of 120 d before transferring them to one of the temperature treatments. We dissected a subset of these logs from each cohort to determine which emerald ash borer larval stages were present in logs prior to rearing. Of the 69 larvae dissected from logs and combined for all sites and years, we determined 94% were diapausing J-larvae, 3% were prepupae, and 3% were immature larvae.

The emerald ash borer-infested logs were placed in growth chambers at 10, 15, 20, 25, 30, 34, or 39°C constant temperatures. For the 10 and 15°C temperature treatments, logs were held in their respective treatments for 90 d before transferring them

Table 1. Mean temperatures (°C), development rates (1/days), number setup (individuals for *Oobius agrili* and logs for emerald ash borer), number of adults that emerged, and number of cohorts for rearing *O. agrili* from the diapausing larval stage to emerged adult, *O. agrili* from parasitoid egg to emerged adult, and emerald ash borer females from the diapausing larval stage to emerged adult

Mean (± SE) temperature (°C)	Mean (±SE) rate (1/days)	No. setup	No. of adults emerged	No. of cohorts
Oobius agrili adult emergence from diapausing larvae				
10.0 ± 0.1	0.00118 ± 0.00005	129	106	2
15.2 ± 0.1	0.00581 ± 0.00005	152	107	3
20.3 ± 0.3	0.02390 ± 0.00034	130	117	3
24.4 ± 0.6	0.03890 ± 0.00019	130	112	3
29.7 ± 0.0	0.05370 ± 0.00042	136	124	3
33.7 ± 0.1	0.04370 ± 0.00059	280	64	3
39.1 ± 0.1	0 ± 0	159	0	2
Oobius agrili adult emergence from parasitoid eggs				
10.1 ± 0	0 ± 0	85	0	2
14.9 ± 0.2	0.00786 ± 0.00009	88	49	3
20.4 ± 0.2	0.03000 ± 0.00015	75	57	2
24.9 ± 0.4	0.04720 ± 0.0040	83	67	3
29.8 ± 0.2	0.06980 ± 0.00043	104	60	3
33.7	0.05790 ± 0.00094	31	27	1
39.1	0 ± 0	49	0	1
Emerald ash borer emergence from diapausing larvae				
10.0 ± 0.1	0 ± 0	10	0	2
15.3 ± 0.3	0.00613 ± 0.00046	14	50	3
19.6 ± 0.1	0.02020 ± 0.00064	18	56	4
24.8 ± 0.3	0.03553 ± 0.0017	17	47	4
30.2 ± 0.2	0.56600 ± 0.00232	19	48	4
34.0 ± 0.4	0.05690 ± 0.00117	17	21	3
39.0 ± 0.1	0 ± 0	8	0	2

Development rates for *O. agrili* 10°C and emerald ash borer 10 and 15°C treatments were estimated by transferring individuals to 25°C after 90 d in their respective treatment temperatures and then calculating development rates using equation 1. All individuals were reared in growth chambers.

to 25°C. Logs held at 10 and 15°C were transferred because preliminary assays indicated emerald ash borer could develop from J-larvae to adults at constant 15°C, but the adults died before emerging (data not shown). We calculated emerald ash borer development rates for 10 and 15°C temperature treatments using equation 1 and used the median development time for emerald ash borer female emergence at 25°C-constant-temperature treatment for the variable $_{i}t_{c25}$. Emerald ash borer adult female emergence from logs was recorded daily, and we repeated temperature assays two to four times using different cohorts of emerald ash borer-infested logs (Table 1).

Emerald Ash Borer Oviposition

We determined emerald ash borer oviposition rates and fecundity over a range of temperatures by placing one male and one female in individual rearing containers within 1 d of emergence from logs held at room temperature (ca. 25°C). Emerald ash borer adults were reared following the procedure described in Rutledge and Keena (2012). Each beetle pair was given fresh *F. uhdei* (Wenzig) Lingelsh. foliage while held in 15, 20, 25, 30, 34, or 39°C constant temperature. We replaced foliage every other day for 30, 34, and 39°C; every 2–3 d for 25°C; and every 3–4 d for 15 and 20°C. Eggs were removed daily and placed in 25°C for 24–48 h to allow embryogenesis to occur. Afterward, we counted the number of fertile (chorion brown and unbroken), infertile (yellow with the chorion unbroken), and defective (chorion broken, not completely formed, or damaged during handling) eggs laid per female per day (Rutledge and Keena 2012). Each week, we randomly reassigned males to different females within their respective rearing temperatures. Adults were maintained in their respective temperature treatments until they died, and we recorded the number of days from female adult emergence from logs to their last day of laying fertile eggs. Temperature assays were repeated using different emerald ash borer cohorts that emerged in August 2017, May 2018, and May 2019 (Table 2).

Rearing Chambers

All phenology experiments were conducted in environmental chambers (Percival Scientific Inc., Perry, IA) under 16:8 (L:D) h photoperiod at ~70% relative humidity, and set at the respective experimental temperature. HOBO Pro temperature data recorders (Onset, Pocasset, MA) were used to measure temperature every 30 min in each of the environmental chambers. We averaged 30-min temperature readings for each temperature treatment replicate to estimate actual chamber temperature for each replicate.

Adult Emergence Functions

F_0 *O. agrili*, F_1 *O. agrili*, and Emerald ash Borer Adult Emergence Functions

Median development rates for adult emergence of emerald ash borer and both generations of *O. agrili* were calculated for each temperature treatment within each replicate as the inverse of the interpolated median development time (1/median days). We used median development rates rather than means due to the inherent tendency of development rates to be skewed right (i.e., a small number of individuals require a very long time to emerge; Sharpe et al. 1977). A nonlinear equation was fitted to the interpolated median developmental rates as a function of temperature for development from 1) diapausing *O. agrili* larvae to emerged F_0 adults, 2) *O. agrili* parasitoid eggs to emerged F_1 adults (F_2 development was assumed to be the same), and 3) emerald ash borer diapausing larvae to emerged adult females. The following equation, which was first described by Logan et al. (1976) and algebraically modified by Régnière (1984), was used:

$$R(T) = P_1\{[1 + \exp(P_2 - P_3 * \tau)]^{-1}] - \exp[(\tau - 1)/P_4]\} \quad (2)$$

where τ = (temperature – T_b)/(T_m – T_b); T_b = low temperature developmental threshold; and, T_m = high temperature developmental threshold. T_b and T_m were predetermined based on the minimum and maximum experimental temperatures. Model convergences were successful for fitting development-rate equations to observed adult emergence rates of emerald ash borer and both generations of *O. agrili* (Fig. 1A, C, and E; Table 3).

We used the 'same rate' method described in Gray (2012) (also see Wagner et al. 1984) to model variability in development rates for emerald ash borer and both generations of *O. agrili* adult emergence. First, all development rates [$R(T)$] for each were normalized by dividing the number of days to develop by the interpolated median days to develop for each temperature and replicate. Then, we fitted the following Weibull function to the normalized rates:

$$F(t) = 1 - \exp[-(x - \lambda/\beta)^{\alpha}] \quad (3)$$

where x represents the normalized development rates [$R(T)$]; λ, β, and α are fitted parameters; and $F(t)$ is the cumulative probability of emergence. Weibull model convergences were successful for fitting the normalized adult development rates (Fig. 1B, D, and F; Table 3).

Emerald Ash Borer Oviposition Functions

Emerald ash borer oviposition was modeled using a modified version of methods from Kim and Lee (2003) and Choi and Kim (2016). In their model, fecundity, oviposition longevity, cumulative oviposition,

Table 2. Mean temperatures (°C), oviposition longevity rates (1/days), eggs per female, number of emerald ash borer females that laid eggs, and number of cohorts for female emerald ash borers reared in growth chambers

Mean (± SE) temperature (°C)	Mean (±SE) emerald ash borer oviposition longevity rate × 10^{-2} (1/days)	Mean (±SE) eggs per emerald ash borer female	No. of emerald ash borer females that laid eggs	No. of cohorts
15.0 ± 0.2		0 ± 0	0	2
19.6 ± 0.1	2.12 ± 0.16	10.5 ± 3.3	19	3
24.8 ± 0.3	2.97 ± 0.22	107.0 ± 13.5	57	3
30.1 ± 0.3	5.61 ± 0.42	108.0 ± 13.2	54	3
34.2 ± 0.5	9.03 ± 0.50	48.5 ± 8.1	41	3
39.1 ± 0.2		0 ± 0	0	2

Oviposition longevity rates were undefined at 15.0 and 39.1°C because no oviposition occurred at these temperatures. Approximately 20 emerald ash borer male–female pairs from each cohort were reared for each temperature treatment.

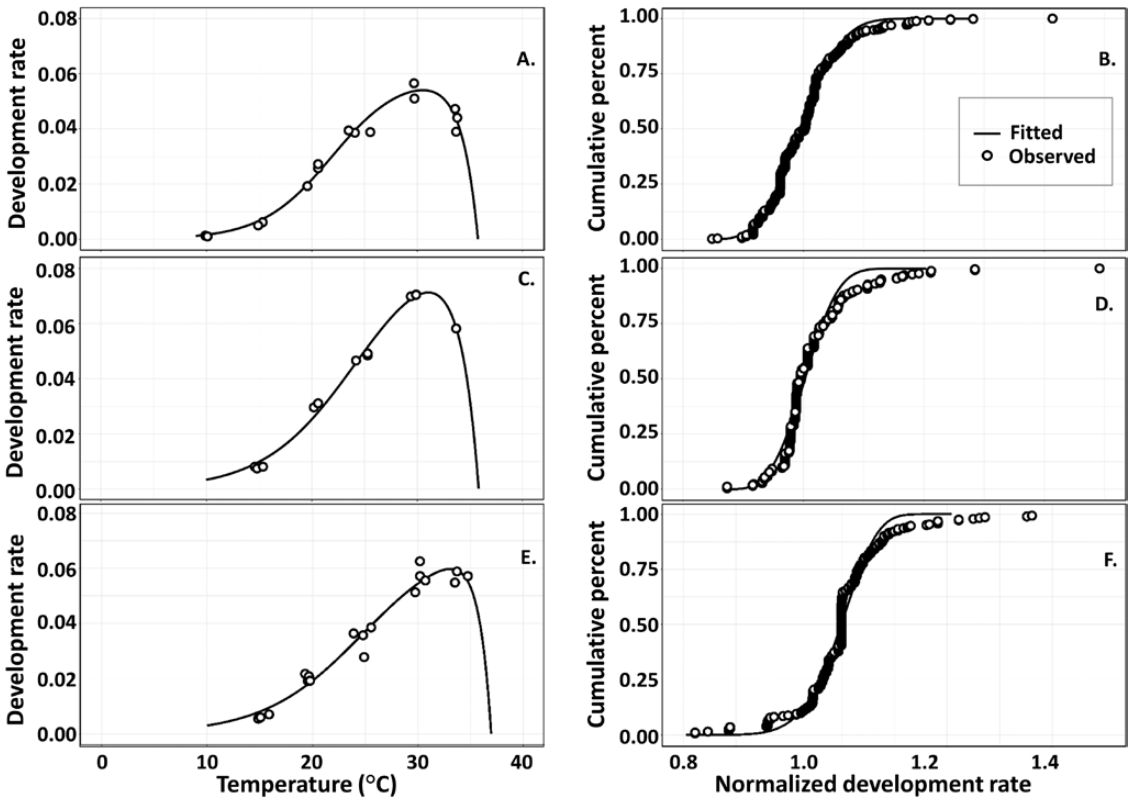

Fig. 1. Functions fitted to observed development rates (1/days) and normalized cumulative development for F_0 *O. agrili* from diapausing larva to emerged adult (A and B), F_1 *O. agrili* egg to emerged adult (C and D), and emerald ash borer diapausing larva to emerged adult female (E and F).

Table 3. Parameter estimates and adjusted R^2 values for development-rate functions and cumulative probability functions for adult emergence from the F_0 *O. agrili* diapausing larval stage, F_1 *O. agrili* parasitoid eggs, and emerald ash borer diapausing larval stage

Insect	Development-rate parameters							Cumulative probability parameters			
	P_1	P_2	P_3	P_4	T_b	T_m	R^2	α	β	λ	R^2
F_0 *O. agrili*	0.060	3.871	9.290	0.0483	40	9	0.988	3.100	0.166	0.848	0.992
F_1 *O. agrili*	0.093	2.808	6.394	0.061	40	12	0.975	3.394	0.144	0.873	0.988
Emerald ash borer	0.071	3.170	6.617	0.037	40	10	0.966	6.231	0.323	0.694	0.972

and cumulative survival were combined to predict daily oviposition as a function of temperature. Our model differs in that survival was terminated on the day that emerald ash borer females stopped laying fertile eggs (i.e., oviposition survival), rather than the day on which females died. This was done because emerald ash borer females often live several weeks in the laboratory after laying their last fertile egg and the objective was to model the emerald ash borer oviposition period rather than adult longevity.

Emerald ash borer adult oviposition longevity is the time in days from adult female emergence from logs to the last day that fertile eggs are laid, including the preoviposition period. A sigmoid function was fitted to the reciprocal of interpolated median days of emerald ash borer oviposition longevity as a function of temperature:

$$r(T) = a + \exp[-(b - T)/c] \quad (4)$$

where $r(T)$ is the oviposition longevity rate at temperature (T) and a, b, and c are fitted parameters. Model convergence of oviposition longevity was successful (Fig. 2A; Table 4). Next, oviposition age (Px_i) was calculated by summing oviposition longevity rates over time (i.e., days) for each female. We then pooled data from all temperatures and cohorts, and calculated cumulative percent oviposition as a function of increasing oviposition age. Equation 3 was fitted to cumulative percent oviposition $p(Px_i)$ as a function of oviposition age (Px_i; Fig. 2B).

Oviposition age was also used to normalize oviposition survival (i.e., the daily proportion of females that had not terminated oviposition of fertile eggs) for each temperature and replicate. These data were pooled and the following modified Weibull function was fitted to the daily proportion of females that were ovipositing fertile eggs [$s(Px_i)$] as a function of increasing oviposition age (Px_i):

$$s(Px_i) = \exp\{-[(Px_i - \lambda)/\delta]\}^{\alpha} \quad (5)$$

where λ, δ, and α are fitted constants. Model convergence was successful for describing cumulative oviposition survival (Fig. 2D).

Emerald ash borer fecundity was modeled by averaging total fertile eggs laid per female within each temperature treatment and cohort. The following function was fitted to the average number of eggs laid per female as a function of temperature:

$$f(T) = \omega * \exp[1 + (\varepsilon - T)/\kappa - \exp(\varepsilon - T)/\kappa] \quad (6)$$

where, $f(T)$ is lifetime fecundity at temperature T; ω is maximum fecundity; ε is temperature when maximum fecundity occurs; and

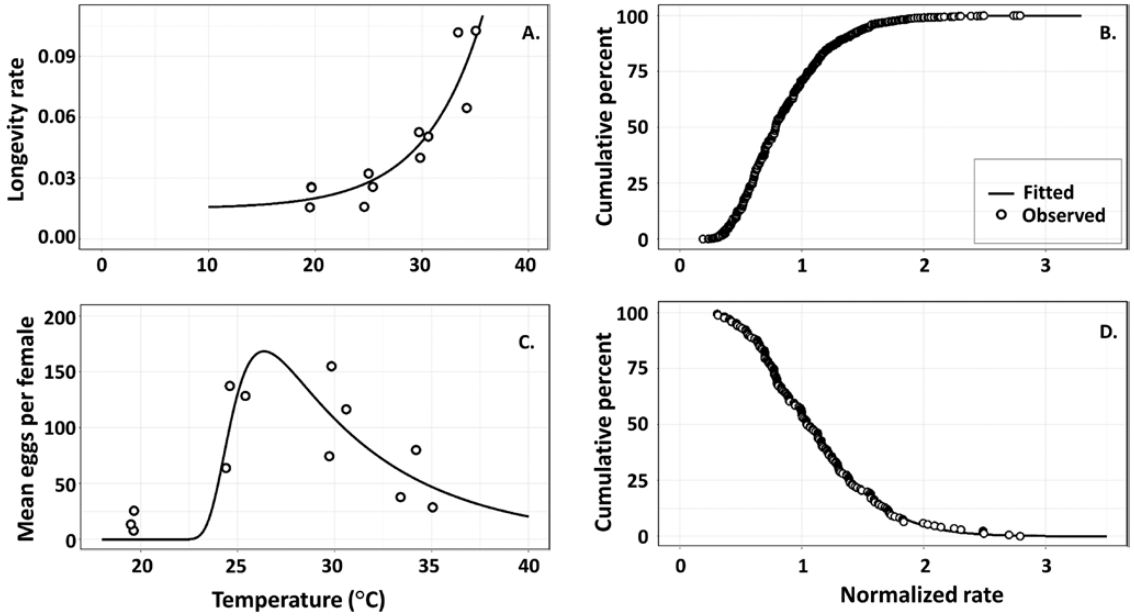

Fig. 2. Functions fitted to observed emerald ash borer oviposition longevity rate (1/days): (A), cumulative oviposition (B), emerald ash borer fecundity (C), and cumulative oviposition survival (D).

Table 4. Parameter estimates and adjusted R^2 for emerald ash borer oviposition functions

Oviposition stage	Parameters and estimates			Adjusted R^2
Oviposition longevity	a = 0.016	b = 46.327	c = 4.588	0.800
Female fecundity	ε = 26.360	κ = 6.000	ω = 73.154	0.601
Cumulative oviposition	α = 1.962	β = 0.736	λ = 0.188	0.998
Oviposition termination	α = 1.836	δ = 0.938	λ = 0.281	0.998

κ is a fitted constant. Model convergence was successful for lifetime fecundity (Fig. 2C; Table 4).

Female fecundity, cumulative percent oviposition, and cumulative oviposition survival were combined to model daily emerald ash borer oviposition [$ro(T)$] as a function of temperature as follows:

$$ro(T) = f(T) \times [p(Px_{i+1}) - p(Px_i)] \times s(Px_i) \quad (7)$$

Parameter estimates for all nonlinear models were determined using the nonlinear least squared method provided in the *stats* package (v3.6.2; R Core Team 2018) that operates in the R statistical environment (R 3.5.0; R Core Team 2018). Adjusted R^2 values were calculated for all fitted models.

Phenology Model Description and Simulations

We combined the rate and cumulative probability equations for the five phenological events described above into a multiple cohort rate summation model that simulates the following: emerald ash borer adult emergence, emerald ash borer oviposition, and emergence of three generations of *O. agrili* adults (i.e., F_0, F_1 and F_2; Supp Data S1 [online only]). We assumed that development rates and the cumulative probability of emergence were the same for F_1 and F_2 adults. Development rates were calculated using hourly temperature data obtained from Cli-MATE (2019) and Michigan State University Enviroweather (2019) for weather stations nearest the sites selected for simulation runs (Fig. 3). All weather stations were within 10 km of study sites. Daily developmental rates and cumulative probabilities were divided by 24 to give hourly rates for simulations (model time step = 1 h). Simulation runs began with all diapausing emerald ash borer and *O. agrili* larvae at the same stage of development (i.e., one cohort each). With each succeeding time step, developmental rates as a function of temperature were summed until each phenological event was complete. Accumulated rates were input into the appropriate cumulative probability function to calculate the proportion of individuals that completed each phenological event. The proportion of the population that completed development during each hourly time step formed a cohort of recruits for the subsequent phenological event and time step. Hence, subsequent phenological events were composed of the flow of cohorts arriving each hour. Cohorts maintained their own rate summation and developmental stage when they transitioned to the next phenological event. Model outputs included emergence curves for each of the five phenological events. The numerical calendar days when day lengths were below the critical day length when *O. agrili* diapause induction should occur (i.e., 14.375 h; Petrice et al. 2019) were also determined for each simulation run. Simulations were performed for four sites over a 3-yr period in south central and northwestern Michigan for comparison with *O. agrili* and emerald ash borer field-trapping data (see section Emerald Ash Borer and *O. agrili* Field Data; Fig. 3). We also performed simulations for four *O. agrili* release locations selected along a north–south gradient in the United States (Duluth, MN [latitude 46.8369, longitude −92.1833]; Indianapolis, IN [latitude 39.8250, longitude −86.2958]; Knoxville, TN [latitude 35.8181, longitude −83.9858]; and Shreveport, LA [latitude 32.4469, −93.8242]) for broader comparisons of spatiotemporal host–parasitoid synchrony

Fig. 3. Map of eastern United States showing sites where *O. agrili* and emerald ash borer phenology were simulated (circles and squares) and where adults of both species were trapped (circles—Michigan only) for model validation.

(Fig. 3). The simulation model was written with GNU Fortran 7.2.0 (Simply Fortran Ver. 2.41, Build 2564, GTK+; Supp Data S1 [online only]).

Emerald Ash Borer and *O. agrili* Field Data

We monitored emerald ash borer and *O. agrili* adult activity at three sites in south central Michigan (Gratiot-Saginaw, Ithaca, MI [latitude 43.2337, longitude −84.4477]; Legg Park [latitude 42.69403, longitude −84.3822] and Harris Nature Center [latitude 42.6965, longitude −84.3752], Okemos, MI, during 2016, 2017, and 2018), and one site in northwestern Lower Michigan (Eastport [latitude 45.1139, longitude −85.3324]) during 2016, where both emerald ash borer and *O. agrili* are established (Fig. 3). We monitored emerald ash borer adult flight period with fluon-coated green funnel traps (Synergy Semiochemical Corp., Burnaby, BC, Canada) baited with *cis*-3-hexenol released at 50 mg/d (Scentry Biologicals, Inc., Billings, MT; Crook et al. 2014). Traps were suspended from the lower- or mid-canopy of ash trees and *cis*-3-hexenol lures were replaced 10 wk after trap deployment. Trap collection cups were filled with propylene glycol (ChemWorld, Taylor, MI) to kill and preserve insects.

We captured *O. agrili* adults in unbaited yellow pan traps attached approximately 1.75 m high to the south-side of ash trees (USDA–APHIS/ARS/FS 2019). We placed a solution of 50:50 food-grade propylene glycol (ChemWorld, Taylor, MI) and H_2O, with a small amount of liquid dish detergent (ca. 2.5 ml/l) to reduce surface tension, in yellow pan traps to capture and preserve insects.

In 2016, 3 funnel traps and 40 yellow pan traps were deployed within a ca. 0.25-ha plot at each of the four study sites (Fig. 3). Funnel traps were spaced at least 20 m apart and arranged randomly within the site on ash trees that displayed little or no canopy dieback. Yellow pan traps were arbitrarily distributed on live ash trees throughout the plot. At the south central sites, we deployed traps on 24–27 May 2016 and removed them 26–30 September 2016. We deployed traps at the northwestern site on 10 June 2016 and removed them 4 October 2016. Trap samples were collected every 2 wk in 2016. In 2017 and 2018, we deployed three funnel traps, as described in 2016, and 10 yellow pan traps on live ash trees that had signs or symptoms of emerald ash borer attack within each plot at the south central sites from 17–18 May to 28–29 September. Trap samples were collected weekly during 2017 and 2018, although the northwestern site (Eastport) was excluded due to logistical constraints. Trap contents were strained through a paint strainer, placed in resealable plastic bags, and frozen until processed.

Comparison of Simulations With Field Data

We calculated percentages of emerald ash borer females and *O. agrili* adults captured by dividing the number of individuals captured for each sample date by total number captured for each respective site and year. We then plotted the percentage of emerald ash borer females and *O. agrili* captured for each sample date over time to compare simulation outputs with field data. The mean absolute numerical calendar date differences between model predictions and trap captures were calculated for 1) the first day of predicted F_0 *O. agrili* and emerald ash borer female adult emergence with the first field trap capture of each; 2) 95% predicted emerald ash borer female emergence and the peak emerald ash borer female trap capture (i.e., sample date when the highest percentage was captured); 3) 95% predicted emerald ash borer oviposition completion and last trap capture of emerald ash borer females; and 4) 95% predicted emergence of each *O. agrili* generation and peak *O. agrili* trap capture. Also, we calculated the predicted percentage of emerald ash borer oviposition completed when 50% adult emergence of each *O. agrili* generation was predicted for each site.

Results

Model Simulations and Trap Capture Comparisons

When we compared simulation results with trap captures at Michigan sites averaged over all sites and years, the predicted first emergence (absolute mean ± absolute SE) of *O. agrili* and the first trap capture of *O. agrili* were within 5.6 ± 2.1 d. The first trap capture of *O. agrili* occurred before model predictions for 2 of 10 comparisons (Table 5; Fig. 4). The predicted first emergence of emerald ash borer females had an absolute mean difference of 6.7 ± 1.7 d from the first capture of emerald ash borer females; the first capture of emerald ash borer females occurred before model predictions for 3 of 10 comparisons (Table 5; Fig. 5). Peak emerald ash borer female trap captures and model predictions of 95% emerald ash borer female emergence differed by 6.8 ± 1.7 d, with peak emerald ash borer female captures occurring before model predictions for 4 of 10 comparisons (Table 5). The last trap capture of emerald ash borer females compared with model predictions of 95% of oviposition complete had an absolute mean difference of 7.4 ± 2.3 d, with the last female emerald ash borer captured before predictions of 95% emerald ash borer oviposition for 4 of 10 comparisons (Table 5). Mean peak *O. agrili* trap captures and the predicted emergence of 95% *O. agrili* adults differed the least for emergence of the F_1 generation (8.2 ± 2.1; Table 5) compared with F_0 (30.4 ± 3.6; data not shown in table) and F_2 (28.9 ± 4.1; data not shown in table).

Spatiotemporal Comparison of Simulations

At all eight sites (i.e., Michigan and north–south gradient) and years, simulated F_0 *O. agrili* adult emergence was predicted to begin 2–5 d (mean = 3.2 ± 0.2) before emerald ash borer oviposition was

predicted to begin (Figs. 4 and 6). When 50% of F_0 adult emergence was predicted, less than 1% of emerald ash borer oviposition was predicted to be complete for any site or year (Figs. 4 and 6). Between 50.1 and 98.0% of emerald ash borer oviposition was predicted to be complete (mean = 63.8 ± 2.0%) when 50% of F_1 adult emergence was predicted, depending on site and year (Figs. 4 and 6). Almost all emerald ash borer oviposition (mean = 99.1 ± 0.1%) was predicted to be complete when 50% F_2 adult emergence was predicted for all sites and years.

As expected, the interaction of critical day length with the predicted emergence of *O. agrili* generations varied among geographic locations (Figs. 4 and 6). At the most northern sites (i.e., Eastport, MI and Duluth, MN), day lengths fell below critical day length just before or after predicted F_1 *O. agrili* adult emergence with the exception of Duluth, MN, in 2017 (Fig. 6B). Day lengths at the south central Michigan sites were longer than critical day length for F_0 and F_1 emergence and below critical day length for the F_2 generation. At the central U.S. locations (Indianapolis, IN and Knoxville, TN), day lengths were longer than critical day length during F_1 and F_2 adult emergence except for the beginning of F_1 emergence at Knoxville, TN, in 2017 (Fig. 6H). Day lengths remained shorter than critical day length during emergence of all *O. agrili* generations at Shreveport, LA (Fig. 6J–L).

Discussion

As the distribution of *O. agrili* in North America expands, interactions of climate and photoperiod could affect host–parasitoid synchrony by altering *O. agrili* emergence, voltinism, and diapause patterns. To examine these effects, we developed a temperature-driven rate summation model to simulate *O. agrili* generations and emerald ash borer oviposition. We then integrated seasonal occurrences of critical day length for diapause induction into the model. Model realism was validated by comparing simulation results with seasonal trap collections of *O. agrili* and emerald ash borer adults from four field sites in Michigan. Model simulations for sites distributed across the current latitudinal distribution of emerald ash borer and *O. agrili* in the United States provide insight on spatiotemporal effects of temperature regimes and day lengths on parasitoid–host synchrony.

Our model predicted that F_0 adult emergence relative to the beginning of emerald ash borer oviposition remained temporally consistent across geographical locations and years (Figs. 4 and 6). However, the model predicted that very little emerald ash borer oviposition would occur during F_0-adult emergence for any location or year. Early emergence of *O. agrili* would temporally position F_0 adults for the earliest possible egg parasitization and presumably ensure F_1 emergence in close synchrony with peak emerald ash borer oviposition. This would also increase the likelihood that some emerald ash borer oviposition would still be occurring if any F_2 adults emerge. Prematurely emerging a few days before emerald ash borer oviposition begins should not reduce the physiological ability of F_0 adults to parasitize emerald ash borer eggs when they become available because *O. agrili* adults can live and parasitize emerald ash borer eggs for several weeks in the laboratory (Hoban et al. 2016, Larson and Duan 2016, Petrice et al. 2019). However, premature emergence could subject adult parasitoids to biotic and abiotic mortality factors before they locate and parasitize emerald ash borer eggs, which could have cascading effects on subsequent generations and parasitism rates.

The *O. agrili* F_1 generation is probably responsible for the majority of emerald ash borer egg parasitism given that predicted emergence of F_1 adults was most synchronized with predicted peak emerald ash borer oviposition compared to other *O. agrili* generations across a north–south gradient. One exception was for the most northern site (Duluth, MN) in 2017, where cool summer temperatures delayed development of the F_1 generation and resulted in emerald ash borer oviposition nearing completion when 50% of F_1 adult emergence was predicted (Fig. 6B). Predicted F_1 adult emergence at the northwestern Michigan site was similar, but slightly less delayed in 2017. If F_1 adult emergence is delayed until emerald ash borer oviposition is almost complete, overall parasitism of emerald ash borer eggs will probably be lower.

Most *O. agrili* were captured in traps before our model predicted F_2 adult emergence. Our model predicts the earliest possible emergence of F_1 and F_2 adults because we did not include *O. agrili* adult longevity and fecundity in our model. One hour after a respective *O. agrili* cohort emerges, the model replaces each individual in that cohort with a parasitoid egg of the subsequent *O. agrili* generation and development of that respective generation begins. Therefore, emergence of F_1 and F_2 adults should continue for several days after our model predicts emergence, given that all generations of *O. agrili* can parasitize emerald ash borer eggs for several weeks after they emerge in the laboratory (Duan et al. 2014, Hoban et al. 2016, Larson and Duan 2016, Petrice et al. 2019). Considering these points, it appears that primarily two *O. agrili* generations (i.e., F_0 adults from diapausing larvae and F_1 adults from nondiapaused larvae) emerge per year in Michigan.

At critical day length, only 50% of the F_1 progeny should enter diapause, increasing to 100% when day lengths fall below 14 h (Petrice et al. 2019). According to our model predictions, emergence of primarily two adult generations seems conceivable for the northwestern Michigan site where critical day length occurred close to predicted F_1 adult emergence, which should presumably have forced most of their progeny into diapause as day lengths continued to decrease. However, at the south central Michigan sites, our model predicted peak F_1 adult emergence well before critical day length was reached. Also, *O. agrili* were relatively abundant in traps at south central Michigan sites during predicted peak F_1 emergence. This should have resulted in a substantial number of eggs parasitized by F_1 adults because emerald ash borer oviposition was also peaking during this period. Therefore, low *O. agrili* trap captures during or after predicted F_2 emergence suggest that most developing F_2 progeny entered diapause earlier than predicted by ambient photophase at south central Michigan sites.

Regardless of site or year, emerald ash borer oviposition was near completion when 50% F_2 adult emergence was predicted. If large numbers of F_2 adults emerged when the model predicted, many would have been biologically stranded because of limited emerald ash borer eggs available for parasitism during this period. Therefore, it appears that in south central Michigan, diapause induction of F_2 larvae prior to ambient photophase falling below critical day length is important for *O. agrili*'s success. On some occasions, *O. agrili* adults were collected at Michigan sites during the period that coincided with model predictions of F_2 adult emergence, suggesting that some developing F_2 progeny perceived day lengths similar to ambient photophases and emerged as adults rather than entering diapause. Also, Abell et al. (2016) determined that some *O. agrili* adults parasitized sentinel emerald ash borer eggs in south central Michigan when F_2 *O. agrili* adults were expected to be present, further supporting, at least for some years, a third generation of *O. agrili* adults may emerge.

Table 5. Numerical calendar day comparisons of model predictions and trap captures for the beginning of *O. agrili* and emerald ash borer adult female emergence with the first individuals of each captured in traps, 95% *O. agrili* F_1 emergence with the peak trap capture, 95% emerald ash borer adult female emergence with the peak emerald ash borer female trap capture, and model prediction of 95% of emerald ash borer oviposition being completed and the last female captured in traps for 3 yr at three sites in south central Michigan (Gratiot-Saginaw, Ithaca, MI; Harris Nature Center and Legg Park, Okemos, MI) and one site northwestern Michigan (Eastport, MI)

		Oobius agrili F_0 emergence begins and first trap capture			*Oobius agrili* F_1 95% emergence and peak trap capture			Emerald ash borer female emergence begins and first trap capture			Emerald ash borer female 95% emergence and peak trap capture			Emerald ash borer 95% oviposition and last female emerald ash borer captured		
Year	Site	Trap	Model	Difference	Trap	Model	Difference	Trap	Model	Difference	Trap	Model	Difference	Trap	Model	Difference
2016	Eastport	175	179	−4	217	220	3	175	175	0	189	193	−4	231	235	−4
2016	Gratiot-Saginaw	173	167	6	200	204	4	160	163	−3	187	176	11	228	218	10
2016	Harris Nature Center	186	163	23	214	200	−14	172	158	14	186	173	13	214	212	2
2016	Legg Park	160	163	−3	214	200	−14	172	158	14	172	173	−1	228	212	16
2017	Eastport	NA	177	NA	NA	227		NA	171	NA	NA	190	NA	NA	239	NA
2017	Gratiot-Saginaw	166	164	2	215	205	−10	159	162	−3	166	175	−9	222	221	1
2017	Harris Nature Center	166	163	3	215	204	−11	166	161	5	186	174	12	215	220	−5
2017	Legg Park	166	163	3	186	204	18	153	161	−8	173	174	−1	221	220	1
2018	Eastport	NA	176	NA	NA	215		NA	169	NA	NA	183	NA	NA	228	NA
2018	Gratiot-Saginaw	165	164	1	200	200	0	156	159	−3	172	175	−3	215	216	−1
2018	Harris Nature Center	172	163	9	200	198	−2	172	158	14	172	172	0	193	214	−21
2018	Legg Park	165	163	2	186	198	12	165	158	7	186	172	14	227	214	13
Mean ± SE absolute difference				5.6 ± 2.1			8.2 ± 2.1			6.7 ± 1.7			6.8 ± 1.7			7.4 ± 2.3

Trapping was not conducted in Eastport in 2017 or 2018 (n = 10–40 *O. agrili* traps and 3 emerald ash borer traps per site).

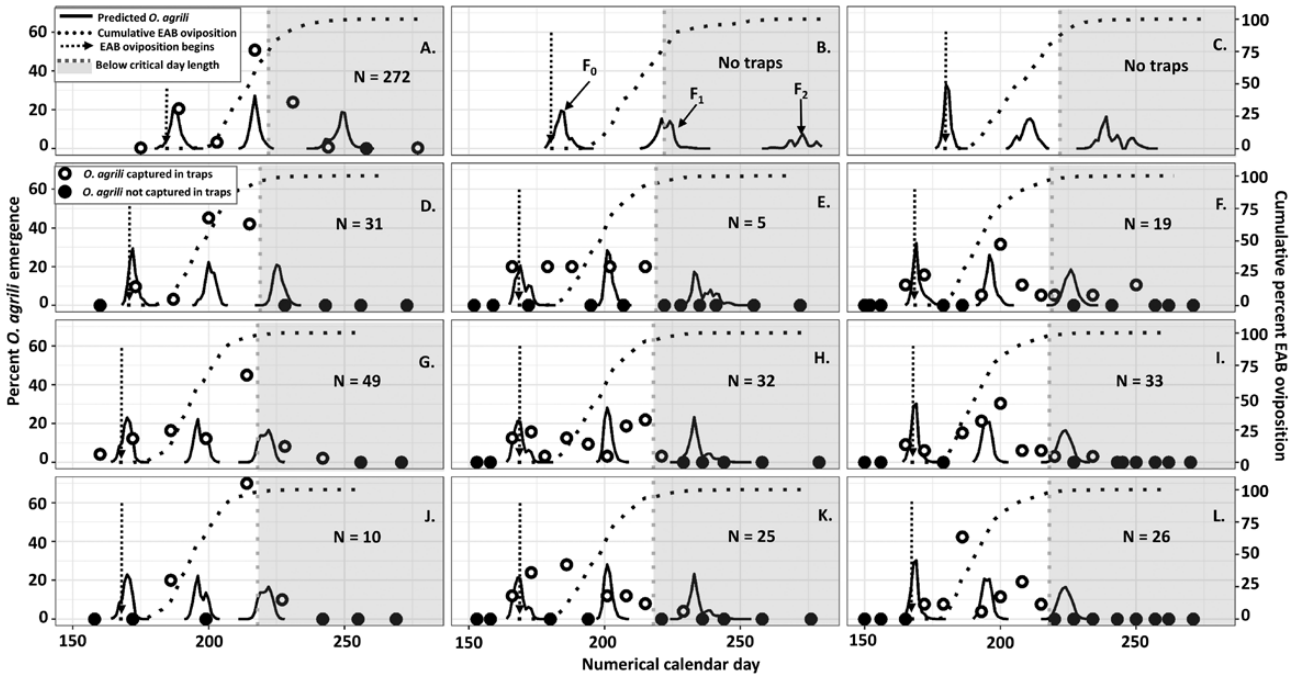

Fig. 4. Percent incidence of predicted adult emergence of F_0, F_1, and F_2 *O. agrili*, cumulative percentage of emerald ash borer oviposition, and *O. agrili* adults captured in yellow pan traps by numerical calendar day over 3 yr for one site in northwestern Michigan (Eastport [A = 2016, B = 2017, C = 2018]), and three sites in south central Michigan (Gratiot-Saginaw, Ithaca, MI [D = 2016, E = 2017, and F = 2018]); Legg Park, Okemos, MI (G = 2016, H = 2017, I = 2018); and Harris Nature Center, Okemos, MI (J = 2016, K = 2017, and L = 2018). *N* is the total number of *O. agrili* captured in traps for each site and year. Gray areas represent periods when day lengths are below critical day length for *O. agrili* diapause induction. See Fig. 3 for location of sites.

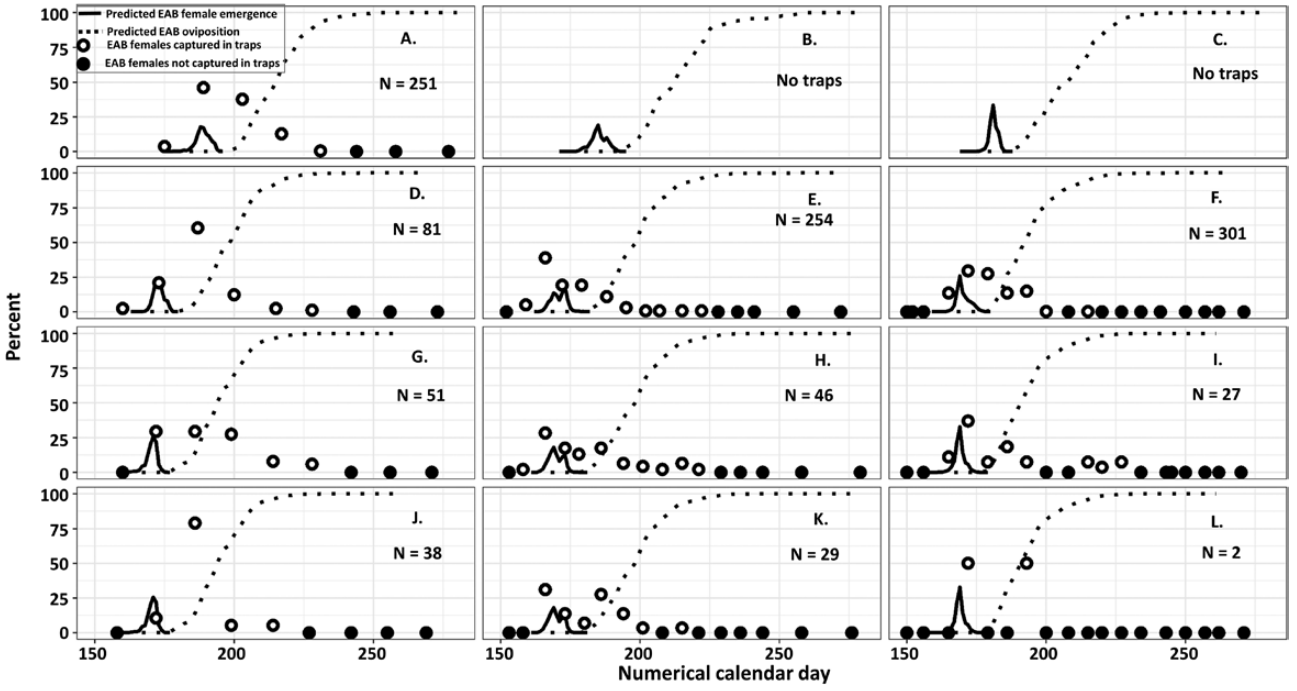

Fig. 5. Percent incidence of predicted emerald ash borer female adult emergence, cumulative percentage of emerald ash borer oviposition, and emerald ash borer adult females captured in funnel traps by numerical calendar day over three years for one site in northwestern Michigan (Eastport [A = 2016, B = 2017, C = 2018]), and three sites in south central Michigan (Gratiot-Saginaw, Ithaca, MI [D = 2016, E = 2017, and F = 2018]; Legg Park, Okemos, MI [G = 2016, H = 2017, I = 2018]; and Harris Nature Center, Okemos, MI [J = 2016, K = 2017, and L = 2018]). *N* is the total number of emerald ash borer females captured in traps for each site and year. See Fig. 3 for site locations.

Multiple factors may have caused most developing F_2 progeny to enter diapause when ambient photophases were above critical day length. Photoperiod exposure of larvae, rather than ovipositing adults, determines diapause induction in *O. agrili* (Petrice et al. 2019). Given that emerald ash borer prefers to oviposit in cracks or between layers of bark (Wang et al. 2010), it is conceivable that

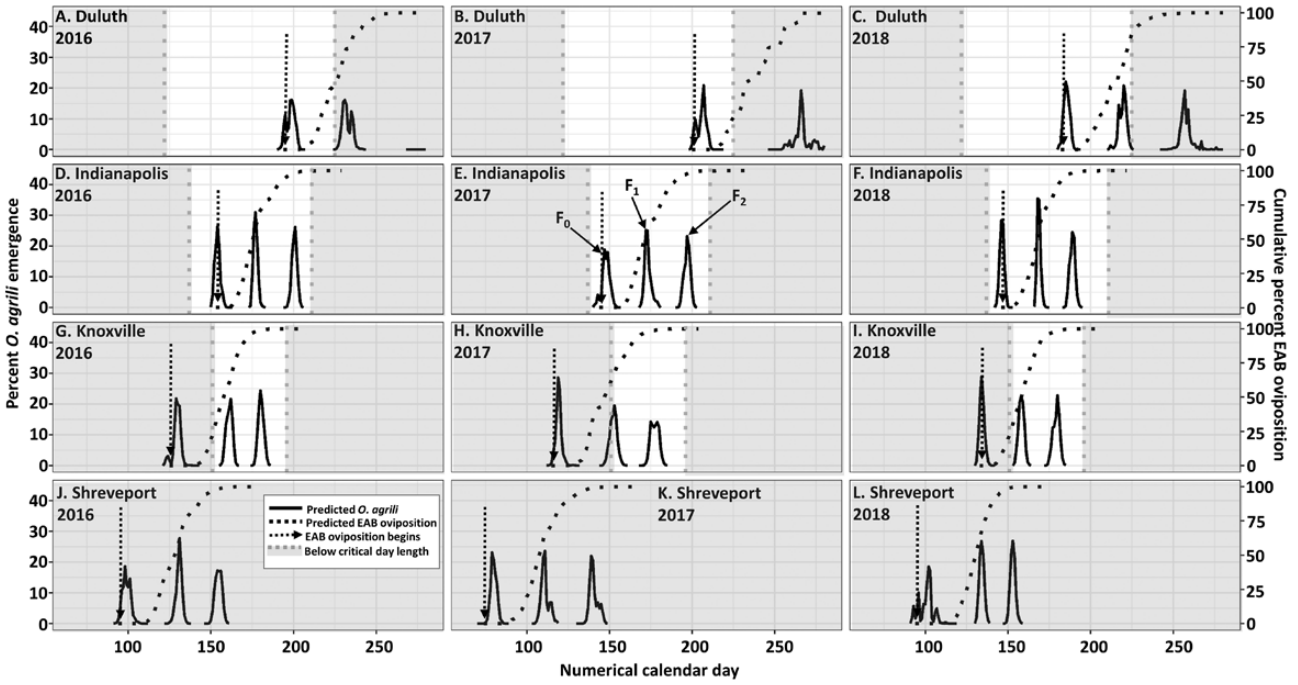

Fig. 6. Percent incidence of predicted adult emergence of F_0, F_1, and F_2 *O. agrili*, and cumulative percentage of predicted emerald ash borer oviposition for 3 yr at four locations along a north–south gradient where *O. agrili* has been released: Duluth, MN (A = 2016, B = 2017, C = 2018); Indianapolis, IN (D = 2016, E = 2017, and *F* = 2018); Knoxville, TN (G = 2016, H = 2017, I = 2018); and Shreveport, LA (J = 2016, K = 2017, and L = 2018). Gray areas represent periods when day lengths are below critical day length for *O. agrili* diapause induction. See Fig. 3 for site locations.

O. agrili larvae in hidden emerald ash borer eggs perceive photophases that are shorter than ambient photophases. Forest canopy cover at study sites could further reduce the amount of daylight that *O. agrili* larvae perceive. Also, Petrice et al. (2019) determined critical day length for *O. agrili* diapause induction at constant 25°C in the laboratory, but critical day length for diapause induction in insects may increase with decreasing temperatures (Li et al. 2008). Therefore, lower nighttime temperatures may lengthen the critical day length that induces *O. agrili* diapause. Alternatively, *O. agrili* larvae may use thermoperiod, in addition to photoperiod, to measure day length as has been demonstrated in several insect species (Beck 1982, Saunders 2014, Wertman and Bleiker 2019). If true, the day lengths measured by thermoperiod could be shorter than those based on ambient photoperiod. One or a combination of these factors are likely responsible for *O. agrili* entering diapause before critical day length is predicted by ambient photoperiod.

It is possible that the critical day length for *O. agrili* diapause induction modulates a bet-hedging strategy for diapause. Parasitoids developing in well-hidden parasitized eggs may be more protected from weather, predators and disease, increasing their probability of surviving as diapausing larvae until the following spring. These well-hidden individuals would perceive day lengths shorter than critical day length and enter diapause, regardless of ambient photoperiod. Alternatively, parasitoid progeny developing in exposed emerald ash borer eggs could suffer higher levels of biotic or abiotic sources of mortality. These individuals would perceive day lengths similar to ambient photophases and emerge as adults; a strategy to avoid mortality during the extended diapause period. However, these adults would risk becoming biologically stranded if no emerald ash borer eggs are present. Critical day length would be important for inducing diapause in exposed parasitoid progeny by preventing them from developing to adults later in the season when few or no emerald ash borer eggs are available. If this hypothesis is true, spatiotemporal day length variation may have less of an impact on *O. agrili* diapause induction.

Model simulations also provide estimates to optimize the timing of *O. agrili* releases in the field. For example, F_0 adults should be released during a short window of time (2–3 wk) beginning when initial emerald ash borer oviposition is predicted. This will allow sufficient time for their progeny to develop and emerge during peak emerald ash borer oviposition. If F_0 adults are released later during emerald ash borer oviposition (i.e., when F_1 adults are predicted to emerge), their progeny that emerge as adults will likely become biologically stranded because most emerald ash borer oviposition will be complete. Releases of F_1 *O. agrili* (or other nondiapaused generations) should be timed to ensure that adults are present when emerald ash borer oviposition is near 50% completion and large numbers of emerald ash borer eggs are present, thereby maximizing both parasitism and the number of progeny that enter diapause. Following these guidelines should help increase *O. agrili* establishment success at release locations.

The preceding discussion assumes that our model accurately characterized the phenology of emerald ash borer and *O. agrili*. Model predictions of *O. agrili* and emerald ash borer phenology aligned reasonably well with field data, however, there were some discrepancies. Factors such as adult longevity, trap efficiency, sampling frequency, weather, and low abundance can confound estimates of when different phenological events, such as peak adult emergence, occurred in the field. These factors can make model validation especially challenging for multivoltine species such as *O. agrili*.

Model accuracy could be affected by variation in diapause development time and termination for emerald ash borer and *O. agrili* diapausing larvae, which are influenced by cold duration (Duarte

2013, Duan and Larson 2019, Petrice et al. 2019). We determined development rates for our model after diapausing individuals of both species were held at constant 4°C for several weeks or months, which may have synchronized diapause development among individuals and subsequent emergence of adults. However, consistent chill period of 4°C does not occur in nature as daily temperatures fluctuate during the overwintering period, which probably affects diapause development times and variability of adult emergence in the field.

Differences between ambient air temperatures and temperatures on the bark surface where *O. agrili* develop, and under the bark where emerald ash borer adults develop may also reduce model accuracy. For example, solar radiation may increase bark temperatures above ambient temperatures for insects developing on the south or west side of trees, resulting in faster development times for some individuals compared to model predictions (Andresen et al. 2001, Potter and Andresen 2002, Vermunt et al. 2012). As expected, Wang et al. (2010) found emerald ash borer adults emerged earlier on the south side of trees compared with the north side.

Intrinsic factors such as the fit of the nonlinear functions that are the foundation of the model may also reduce model accuracy. For example, the emerald ash borer adult emergence cumulative probability function prematurely predicted the end of emerald ash borer emergence when compared with laboratory data (Fig. 1F) and, not surprisingly, emerald ash borer peak trap captures often occurred after the model predicted emerald ash borer emergence had ended (Table 5). Also, trap captures at our Michigan sites suggest that our model exaggerated the length of emerald ash borer oviposition, given that the last emerald ash borer females often were captured closer to 95% predicted emerald ash borer oviposition rather than 100% predicted emerald ash borer oviposition (Fig. 5). This overestimate may partially be attributed to artificial laboratory rearing conditions that may promote oviposition longevity.

The model developed in this study provides insight on the interactions of temperature and day length on the phenological synchrony of *O. agrili* and emerald ash borer at different geographic locations. However, more validation is necessary, especially at a larger spatial scale, to confirm that both species will respond similarly in different climates. For example, it is possible that warmer winter temperatures in southern regions may affect diapause completion, which could alter emergence patterns of both species. Also, ambient photophase does not appear to be a good predictor of when most *O. agrili* enter diapause. It is possible that the critical day length functions as a bet-hedging strategy for *O. agrili* diapause induction, which may reduce the effects of spatiotemporal-photoperiod variation on *O. agrili* population dynamics. A better understanding of how *O. agrili* measures day length in the field is needed to determine how *O. agrili* voltinism and diapause patterns will be affected in novel geographic locations. Additionally, integrating *O. agrili* longevity and fecundity into this model would enhance its utility and realism.

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

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