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Comparing Asian Gypsy Moth [*Lymantria dispar asiatica* (Lepidoptera: Erebidae) and *L. dispar japonica*] Trap Data From East Asian Ports With Lab Parameterized Phenology Models: New Tools and Questions

R. Talbot Trotter III,[1,4] Samita Limbu,[2] Kelli Hoover,[2] Hannah Nadel,[3] and Melody A. Keena[1,]

[1]U.S. Forest Service, Northern Research Station, 51 Mill Pond Road, Hamden, CT 06514, [2]Department of Entomology and Center for Chemical Ecology, The Pennsylvania State University, 501 ASI Building, University Park, PA 16802, [3]USDA Animal and Plant Health Inspection Service, PPQ S & T, 1398 West Truck Road, Buzzards Bay, MA 02542, and [4]Corresponding author, e-mail: robert.t.trotter@usda.gov

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Abstract

Management of the European gypsy moth [*Lymantria dispar dispar* (Linnaeus)] in North America has benefited from more than a century of research. The East Asian strains of the gypsy moth, however, bring new challenges including multiple subspecies (*Lymantria dispar asiatica* Vnukovskij and *Lymantria dispar japonica* Motschulsky), broad distributions across heterogeneous habitats, and a lack of data on the variation in the phenology of source populations, which may affect risk. To address these issues, published phenology parameters for eight populations of Asian gypsy moth were used to develop eight strain-specific agent-based phenological models. These models were applied to 47 ports in East Asia where the Asian gypsy moth is native, and output was compared with available trap data to assess the role of interpopulation variation in phenological parameters in predicting moth flight among varied locations, assess variation in the performance of models among years, and assess the importance of modeling phenology using parameters from a 'local' moth population. Variation in phenological parameters among the eight populations yielded variation in predicted flight times among the 47 ports analyzed, and the use of 'local' populations did not generally improve model fit. Model accuracy varied substantially among ports and among years within some ports. The larva-to-adult agent-based models described here have utility in estimating flight periods for some ports in their current form, but variation in model quality across the landscape suggests that there is potential for unsampled and unparameterized moth populations and factors that remain to be quantified.

Key words: Asian gypsy moth, agent-based model, phenology simulation

With growing international trade, the potential to move species from native environments to novel locations continues to expand (Seebens et al. 2018), and new tools will continue to be required to identify and mitigate these risks. The risks and challenges associated with subspecies, strains, and populations of the Asian gypsy moth (*Lymantria dispar asiatica* Vnukovskij and *Lymantria dispar japonica* Motschulsky) highlight both the need for these tools and some of the challenges associated with developing them. A century

of research on the Asian gypsy moth's close relative, the European gypsy moth [*Lymantria dispar dispar* (Linnaeus)], has provided insight into the potential damage the Asian gypsy moth may cause to North American landscapes if allowed to establish.

Since its introduction in the town of Medford, MA, in the 1890s, the European gypsy moth has spread through eastern North America (Liebhold et al. 1992, 1997) where it feeds on more than 300 species of trees and shrubs (Liebhold et al. 1995), defoliating on average

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more than a quarter of a million hectares per year (APHIS 2016). Ecological damage, health impacts, and management efforts focused on the European gypsy moth cost the public an estimated $253 million annually (Aukema et al. 2011), and long-term impacts on forest development (Morin and Liebhold 2015) will probably carry these costs into the future.

The Asian gypsy moth offers new challenges and risks. Asian strains of the gypsy moth have a broader host range (Baranchikov 1988) that includes more than 500 species from more than 100 families (APHIS 2016), and unlike the European gypsy moth, Asian gypsy moth females can fly (Keena et al. 2008, Iwaizumi et al. 2010, Schaefer and Strothkamp 2014). If introduced to North America, the combination of an expanded host range and flighted females would probably allow the moth to spread quickly across North American landscapes.

Several factors interact to create a high potential for Asian gypsy moths to be moved internationally. The moth is native to East Asia and can be found in many of the shipping ports along the coasts of eastern Russia, eastern China, the Republic of Korea, and Japan where large quantities of goods are staged and shipped. The majority (>90%) of nocturnally flying females have been found to be mated (Schaefer and Strothkamp 2014), and female Asian gypsy moths are attracted to bright lights (Wallner et al. 1995). Because shipping terminals are typically well lit, mated female moths can be drawn into brightly lit facilities where they can place viable egg masses on shipping containers, cargo, vehicles, and the ships themselves (APHIS 2016). This infested material is then moved internationally, delivering the Asian gypsy moth to new environments (Gray 2010, 2016).

Based on the recognized risk of moving infested materials, Asian gypsy moth movement on vessels and cargo to North American ports is regulated under the North American Plant Protection Organization (NAPPO) regional standards for phytosanitary measure (RSPM) number 33 (NAPPO 2017). Much of the risk is managed through the inspection of ships and cargo both at the source ports and at the receiving ports in countries that regulate shipments from infested locations. In the United States, the requirements to inspect individual ships is determined in part by whether the ship has visited a high-risk port (i.e., is known to be infested with the Asian gypsy moth) during a high-risk period (the flight period for the Asian gypsy moth) within the previous 24 mo. High-risk periods for source ports are defined by the United States Department of Agriculture, Special Procedures for Ships Arriving from Areas with Asian Gypsy Moth (AGM; https://www.aphis.usda.gov/plant_health/plant_pest_info/gypsy_moth/downloads/AGM_Procedures.pdf) and are based on defined calendar dates. To continue to improve biosecurity while minimizing unnecessary impacts on trade, there is a need for phenologically based models for the multiple strains of the Asian gypsy moth, and to assess the utility of these models in predicting both adult flight, and the timing of second instars (the stage at which population suppression efforts are usually applied) across multiple and heterogeneous source ports.

Phenology models are based on the concept of physiological time and typically use readily monitored parameters such as temperature to estimate the rate and timing of development in poikilotherms such as insects (Allen 1976; Logan et al. 1976, 1991; Beck 1983; Casagrande et al. 1987; Sheehan 1992; Gray et al. 2001; Gray 2004, 2009, 2010, 2016, 2018). Although the structures of temperature-driven phenology models vary, they are generally based on a set of phenological parameters including the lower and upper critical temperatures (L_{ct} and U_{ct}, respectively), which define a thermal envelope within which the organism can develop, and a measure of accumulated heat (commonly heating degree-days, hereafter HDD) used to estimate cumulative development (Allen 1976). Parameters can vary among life stages (Logan et al. 1991; Sheehan 1992; Gray 2001, 2018; Sharifi et al. 2016), genders (Sheehan 1992, Limbu et al. 2017), and populations within a species (Limbu et al. 2017). Collectively, these parameters have been used to develop phenology models to estimate the timing of key events such as egg hatch, pupation, and flight for a broad range of species (examples can be found at http://ipm.ucanr.edu/WEATHER/index.html and https://www.usanpn.org/home).

Temperature-driven phenology models for the European gypsy moth, *L. dispar dispar* (Linnaeus), have been developed and applied to eastern North America (Logan et al. 1991, Sheehan 1992, Gray 2001). More recently, work by Gray (2004, 2010, 2016), Pitt et al. (2007), and Magarey et al. (2015) has applied the gypsy moth life-stage model (GLS, which is based on the European gypsy moth) and GLS-based parameters to estimate the risk posed by the Asian gypsy moth (*L. dispar asiatica* Vnukovskij and *L. dispar japonica* Motschulsky).

Although these models have provided new information that can benefit the management of introduction risk for the Asian gypsy moth, they include a number of limitations. First, GLS is based on a single set of parameters for the European gypsy moth (a limitation noted by Pitt et al. 2007) and does not account for variation among subspecies and populations. Second, the application of the model as described by Magarey et al. (2015) uses climate records averaged over a 10-yr period and does not assess potential interannual variation in model utility. Magarey et al. (2015) also assume that flight continues for 2 mo after reaching a fixed heating degree-day threshold. Although this does provide a binary indication of moth presence (which is critical from a risk management perspective), it limits the comparison of model output and flight trap data to the first and last time steps for which moth flight is inferred and does not account for variation in moth abundance through the flight season. Finally, suppression efforts for gypsy moths often depend on knowing the timing of key larval instars (typically the second; Reardon 1994), and current models are focused primarily on identifying the timing of adult flight.

Here, we seek to reduce this knowledge gap by developing strain-specific, multi-instar phenology models for populations of the Asian gypsy moth and assess their applicability to shipping ports in East Asia. Recent work by Limbu et al. (2017) evaluated eight populations including six populations of *L. dispar asiatica* from Russia, the People's Republic of China, and the Republic of Korea, and two populations of *L. dispar japonica* from Japan. These lab-based studies revealed significant variation in phenological parameters among populations, as well as variation between male and female moths within populations. The incorporation of sex-based effects in phenology models for ports in East Asia may have value due to the disconnect between the factor that is monitored in ports (male flight) and the factor of interest (mated female dispersal and oviposition).

Although there is substantial work to be done to assess these population-specific Asian gypsy moth phenology parameters and to compare the results with predictions based on other tools such as GLS, in this study we focus the scope of analysis on the use of the phenology data collected in Limbu et al. (2017) to address three basic but fundamental questions. First, we seek to develop a larva-to-adult, individual-based phenology model using parameters from both sexes and all eight populations and to compare the predicted male flight periods with the observed patterns of male flight based on trapping data collected in 47 ports in East Asia. Second, we seek to assess whether the application of 'local' moth populations to ports

in East Asia results in improved estimates of the flight period. Finally, we use these models to begin to assess their potential application in predicting Asian gypsy moth flight among ports in East Asia. If models can reasonably predict moth flight by simulating the development of each larval and pupal stage, it may be possible to predict the presence of other stages such as second instars, providing opportunities for the use of additional suppression tools such as the application of biopesticides. Although accuracy in these larva-to-adult models could be informative for managers, errors, biases, and deviations in model accuracy can also be informative, as they can indicate the need to identify and integrate additional factors in the models.

Materials and Methods

Asian Gypsy Moth Population Sources

The phenology models described here are based on published development parameters for eight populations of the Asian gypsy moth. Six of the populations represent *L. dispar asiatica*, with three populations sampled in the People's Republic of China, two in Russia, and one in the Republic of Korea. Two populations of *L. dispar japonica* were sampled in Japan. Voucher specimens from each population are archived at the Yale Peabody Museum of Natural History, Entomology Division, New Haven, CT. Additional information on the populations and methods used to identify phenology parameters are described in greater detail in Limbu et al. (2017) and are only briefly summarized here.

At the time of the laboratory assays, colonies had been maintained for periods ranging from 4 to 30 generations under quarantine conditions at the United States Department of Agriculture (USDA) Forest Service Insect Quarantine in Ansonia, CT. Each generation of moths was initiated with a mix of 100 egg masses from the previous generation to help retain genetic diversity and limit laboratory adaptation. Temperature-dependent development rates were quantified experimentally for each post-egg life stage for each of the eight populations by rearing cohorts of 100 individuals at five constant

temperatures (10, 15, 20, 25, and 30°C) on a standardized artificial diet. The development of individuals was monitored, and the dates on which individuals molted or eclosed were recorded. Standard methods were used to identify the lower critical temperature for development (L_{ct}), the upper critical temperature for development (U_{ct}), the number of heating degree-days required to complete development (HDD$_{req}$), and the distribution of variance in HDD$_{req}$ in each life stage (HDD$_{var}$; see Limbu et al. 2017). Moths developed through a minimum of four and a maximum of eight instars before proceeding to the prepupal and pupal stages. Additionally, data from Limbu et al. (2017) were reanalyzed to determine the proportions of each population for which the fourth–eighth instars represented the ultimate larval instar. This parameter was included in the phenology models using the parameter (I_r).

Phenology Model Structure

The models described here use an agent-based structure in which simulated individual moths (rather than cohorts, e.g., Sheehan 1992) transit through each instar or life stage using a structure similar to what is described in Trotter and Keena (2016) and Kappel et al. (2017). The development of individuals is regulated by five life stages, population, and sex-specific phenology parameters (U_{ct}, L_{ct} HDD$_{req}$, HDD$_{var}$, I_r) and the accumulation of heating degree-days. Heating degree-days are calculated daily (the time step used in the model) from daily minimum and maximum temperatures using the modified sine wave method described by Allen (1976).

Each population includes parameters for each of one to seven standard instars (instars that are not followed by prepupal development, and are common to both males and females), parameters for each ultimate instar based on sex, and prepupal and pupal development based on sex. The full set of strain, sex, and life-stage-specific parameters used for each of the eight populations are provided in Supp Table S1 (online only); an example set of parameters for a moth population from Russia (R1) is provided in Table 1.

Table 1. Life-stage specific phenology parameters used to simulate the development of Asian gypsy moths from the R1 moth population

Population	Sex	Instar	HDD$_{req}$	HDD$_{reqsd}$	U_{ct}	L_{ct}	Ratio
R1	All	1	84.79	14.96	31.5	8.50	0
R1	All	2	69.59	15.40	32.0	7.49	0
R1	All	3	59.26	21.20	32.0	9.70	0
R1	All	4	68.45	16.25	32.0	9.90	0
R1	All	5	90.86	25.64	31.5	9.57	0
R1	All	6	125.65	—	31.5	9.57	0
R1	All	7	—	—	—	9.57	0
R1	F	4U	—	—	—	6.75	0
R1	F	5U	212.69	21.95	31.5	6.75	0.95
R1	F	6U	190.81	26.76	31.5	7.34	0.99
R1	F	7U	227.25	—	31.0	7.34	1
R1	F	8U	—	—	—	7.34	1
R1	F	PP	19.03	5.26	31.5	10.19	1
R1	F	P	204.93	13.23	31.5	7.68	1
R1	M	4U	161.31	15.14	31.5	9.36	0.05
R1	M	5U	173.20	20.86	31.5	7.26	0.99
R1	M	6U	192.61	48.07	31.5	7.26	1
R1	M	7U	—	—	—	7.26	1
R1	M	8U	—	—	—	7.26	1
R1	M	PP	19.99	5.71	31.5	9.14	1
R1	M	P	215.41	17.66	31.5	7.93	1

Each population includes 14 potential life stages (depending on sex and number of instars), though some instars or stages do not occur in some populations, as indicated by the missing values (dashes) in the table. Parameters for the other seven populations are available online in Supp Table S1 (online only).

The conceptual structure for the model is generally simple. An individual moth (agent) is initiated as a neonate first instar with no accumulated development on the first day of the simulation, corresponding to 1 January. This starting scenario places the population under the assumption that first instars will initiate development as soon as thermal conditions are suitable (Table 1 and Supp Table S1 [online only]). There are several reasons this structure was used. First, the lower critical temperatures that allow first-instar development (Table 1 and Supp Table S1 [online only]) are close to the lower temperature at which larvae become active and climb trees to feed (<10°C), although rain can delay this behavior (McManus 1973). Second, the assumption that first instars develop as soon as the temperature allows limits potential timing bias in the model to an acceleration bias (i.e., the model predicting development and flight earlier than what is observed in the field). Because the moths are developing as early as possible, the model does not foster lags (i.e., late flight predictions). From a conceptual perspective, this limits the directionality of the bias in the model, and from an application perspective, this makes the model 'conservative' by reducing the chance of missing early moth flight. Finally, the regulation of European gypsy moth egg development is known to be complex (Gray et al. 2001; Gray 2004, 2009, 2010, 2018), and phenological data for the eggs of Asian strains of the gypsy moth are not available. Rather than using the egg parameters for the European strain, which would add inter-subspecies variation, the model is simplified by leaving eggs out of the model. Also, by initiating individuals as first-instar larvae, the utility of a simplified larva-to-adult model (without the inclusion of a complex egg stage) can begin to be assessed.

Each individual moth is assigned a required number of HDD units to complete the first instar, based on the mean required HDD (HDD_{req}) plus a value drawn from a randomized normal distribution based on the variation observed in the population (HDD_{var}),

corresponding to the variation observed in Limbu et al. (2017). On each sequential day in the simulation, the number of accumulated heating degree-days are calculated using the population-specific first-instar parameters (U_{ct} and L_{ct}) and the daily minimum and maximum temperature for the specified date and location. At the end of each day, the required number of heating degree-days for the individual to complete the first instar (HDD_{req} + HDD_{var}) is compared with the accumulated HDD. If (HDD_{req} + HDD_{var}) > HDD, the individual is reclassified as a second instar. The process is then repeated for the individual using second-instar parameters and variance estimates, with day 1 of the second instar being set to the last day of the previous instar plus one. Individuals proceed through each instar and development stage until either 1) the adult emerges indicating moth flight or 2) day 365 is reached. On day 365, the individual is assumed to have failed to complete univoltine development.

This agent-based approach provides several advantages including the ability to introduce variable behaviors to individuals such as plasticity in the number of required instars among individuals, the flexibility to provide instar and life-stage-specific phenology parameters, and the introduction of variation in the required heat accumulation and critical temperatures among individuals in the population. The model also provides flexibility for the addition of new parameters and behaviors as they are identified and allows the model to be readily adapted to new data. A key parameter that remains to be assessed is the role of autocorrelation in the variation in development time among instars for a given individual. In its current state, the model assumes independence among instars, and the validity of this assumption will be addressed in subsequent analyses.

The output table generated by the model provides an estimate of population structure at any given time slice (date) as well as an estimate of the temporal windows when a given life stage is present. The phenology model described here (AGMLT v1, see
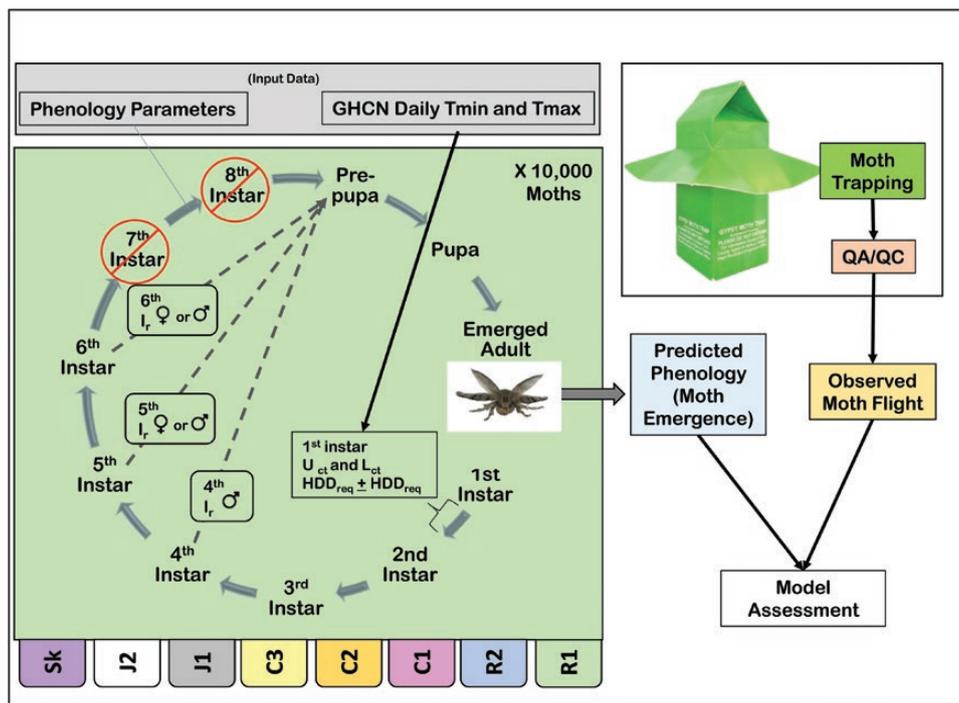
Fig. 1. The agent-based phenology model is represented by the grey box to the left, and demonstrates multiple paths through different numbers of instars which each of the 10,000 individual simulated moths may follow. Tabs below the box represent the multiple populations, each of which has population-specific parameters and numbers of instars. Boxes along the right show the process flow for the assessment of the model.

Supp File S2 [online only]) was developed using MatLab R2018a (9.4.0.813654, The MathWorks, Inc., Natick, MA) and MatLab Compiler and is available both in Supp File S2 (online only) and from the corresponding author. This software can be run from the source code or as a stand-alone program (AGMLTv1.exe). Required data inputs include minimum and maximum temperature values (or a GHCN-Daily station ID value used to retrieve data from the National Centers for Environmental Information), and instarspecific upper and lower critical temperatures, heating degree-day requirements, estimates of variance, and molt ratios (i.e., the proportions of instars 4, 5, 6, and 7 that will proceed directly to pre-pupae).

To facilitate comparison of the eight population-specific parameter sets and to assess the role of interport and interannual variation in temperatures, simulations of 10,000 individuals were carried out for each port using both genders of each of the eight moth populations, using daily temperature records for each of the years for which moth trap and temperature data were available for a given port. This combination of factors yields 2,768 simulations (Fig. 1).

Moth Trap Data

International agreements developed in support of RSPM 33 have prompted long-term pheromone trapping studies using Disparlure baited traps at numerous ports in East Asia, including ports in

Table 2. Shipping ports with Asian gypsy moth trap data (trap-years provided) and the Global Historical Climatology Network weather stations used to simulate moth development for each port

Country	Port	Station used	Trap-years	Local population
Republic of Korea	Donghae	KSM00047105	2011–2015	SK
Republic of Korea	Okgye	KSM00047105	2011–2015	SK
Republic of Korea	Incheon	KS000047112	2011–2015	SK
Republic of Korea	Pyongtaek	KS000047112	2012–2015	SK
Republic of Korea	Busan	KSM00047159	2012–2015	SK
Republic of Korea	Pohang	KSM00047138	2014–2015	SK
Republic of Korea	Ulsan	KSM00047159	2011–2015	SK
Republic of Korea	Gunsan	KS000047165	2015	SK
Republic of Korea	Mokpo	KS000047165	2012–2015	SK
Republic of Korea	Gwangyang	KSM00047168	2012–2013	SK
Republic of Korea	Yeosu	KS000047165	2012–2015	SK
Republic of Korea	Masan	KSM00047159	2015	SK
Republic of Korea	Dangjin	KS000047112	2013–2015	SK
Republic of Korea	Yeongilman	KSM00047138	2014	SK
Republic of Korea	Onsan	KSM00047159	2013–2015	SK
Republic of Korea	Daesan	KS000047112	2013–2015	SK
Japan	Kokura	JA000047807	2005–2007	SK
Japan	Ube	JA000047784	2005–2007	J2
Japan	Oita	JA000047815	2005–2007	J2
Japan	Hirosihima	JA000047765	2005–2007	J2
Japan	Matsunaga	JA000047767	2004–2007	J2
Japan	Hannan	JA000047772	2004–2007	J2
Japan	Tsuruga	JA000047616	2004, 2006–2007	J2
Japan	Shimizu	JA000047656	2005–2007	J1
Japan	Kanazawa	JA000047600	2004–2007	J2
Japan	Chiba	JA000047640	2004–2007	J2
Japan	Fushiki	JA000047600	2004, 2006–2007	J2
Japan	Toyama-shinko	JA000047600	2004–2007	J2
Japan	Sakata	JA000047520	2004–2007	J1
Japan	Hachinohe	JA000047575	2005–2007	J1
Japan	Nagahama	JA000047574	2004–2005, 2007	J2
Japan	Aomori	JA000047576	2005–2007	J1
Japan	Hakodate	JA000047430	2004–2007	J1
Japan	Tomakomai	JA000047424	2005–2007	J1
Japan	Otaru	JA000047412	2004–2007	J1
Russia	Vladivostok	RSM00031969	2013–2017	R2
Russia	Nakhodka	RSM00031987	2013–2017	R2
Russia	Vostochny	RSM00031987	2012–2017	R2
Russia	Russky Island	RSM00031969	2013–2017	R2
Russia	Olga	RSM00031959	2013–2017	R2
Russia	Slavyanka	RSM00031969	2013–2017	R2
Russia	Zarubino	RSM00031969	2013–2017	R2
Russia	Posyet	RSM00031969	2013–2017	R2
Russia	Plastun	RSM00031909	2013–2017	R2
Russia	Vanino	RSM00031770	2013–2015	R2
Russia	Kozmino	RSM00031987	2013–2017	R2
Russia	Korsakov	RSM00032150	2014–2015	R2

Additional weather station data are available at ftp://ftp.ncdc.noaa.gov/pub/data/ghcn/daily/ghcnd-stations.txt.

the People's Republic of China, Russia, Japan, and the Republic of Korea. Annual trapping provides regulators with information about moth presence and abundance in each port and facilitates the monitoring of ships and cargo from ports where moth populations are high. Asian gypsy moth trap data were compiled from United States Department of Agriculture Forest Service (USDA FS) and Animal and Plant Health Inspection Service (USDA APHIS) international cooperators and included moth trap-catch data for 51 ports. The number of years with trap records varied among ports, ranging from a minimum of one to a maximum of six. To be included in these analyses, the data for a given year had to include at least three dates on which moths were detected in traps, with a total accumulation of at least 10 moths over the trapping period. These limits yielded data for a total of 173 individual years distributed among 47 of the ports (hereafter referred to as port–years; Table 2). Traps were checked at time intervals that varied among locations and years, with trap check frequency ranging from daily to once every 10 d. Trap records provided the total number of male gypsy moths in the trap on the date the trap was checked. Ports varied in the numbers of traps used (both among ports and among years). To mitigate the potential influence of variable sampling effort on patterns of moth detection, trap-catch values were standardized as a portion of the total number of moths trapped within a given port and year.

Temperature Records

The minimum and maximum daily temperatures used as input were obtained from the National Oceanic and Atmospheric Administration (NOAA) National Centers for Environmental Information (NCEI, formerly known as the National Climatic Data Center, NCDC) Global Historical Climatology Network-Daily (GHCND) database (ftp://ftp.ncdc.noaa.gov/pub/data/ghcn/daily, accessed 8 March 2019). Weather stations were selected based on their proximity to the trap locations and the availability of minimum and maximum daily temperature values for the period spanning 1 January 1981–31 December 2018 and are listed in Table 2. Some weather stations include data gaps ranging from a single day to multiple years. To fill these data gaps, mean values for the missing dates were calculated from available values for the same dates from 1981 through 2010 (inclusive), corresponding to the current time period used to calculate the most recent 30-yr climate normals. A list of the included 47 ports and their corresponding weather stations is provided in Table 2.

Statistical Analyses

To assess the role of variation among populations, the simulated flight times estimated for each of the eight, male population-specific phenology models were compared with the observed male flight times based on moth trap data. Each of the sex- and population-specific models
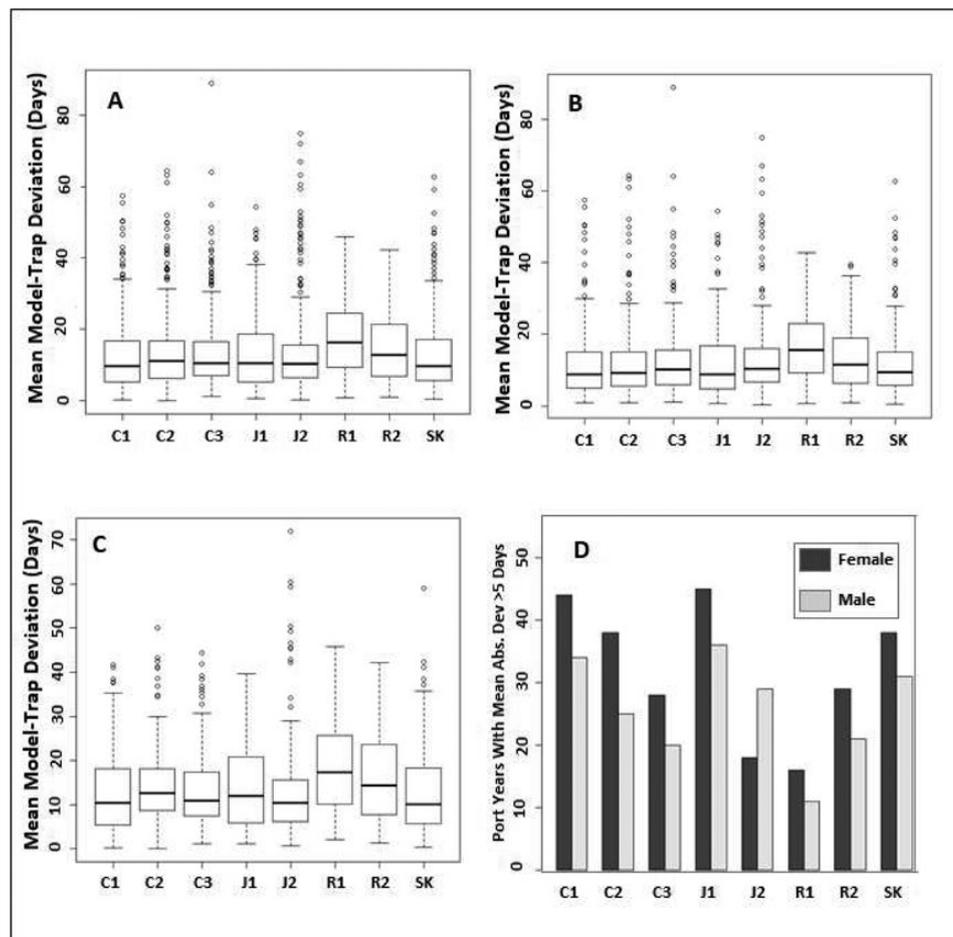
Fig. 2. (A–C) The distribution of the mean absolute deviations between the modeled timing of moth flight and the observed moth flight based on trapping data for each of the 173 port–years from application of each of the eight population-based phenology models. Populations are shown with sexes pooled (A) and separately (B and C). Variation among populations and sexes is statistically significant. (D) A 'slice' of these data, based on categorizing deviations based on model fit that is within 5 d of the trap data. Note the variation among sexes and populations.
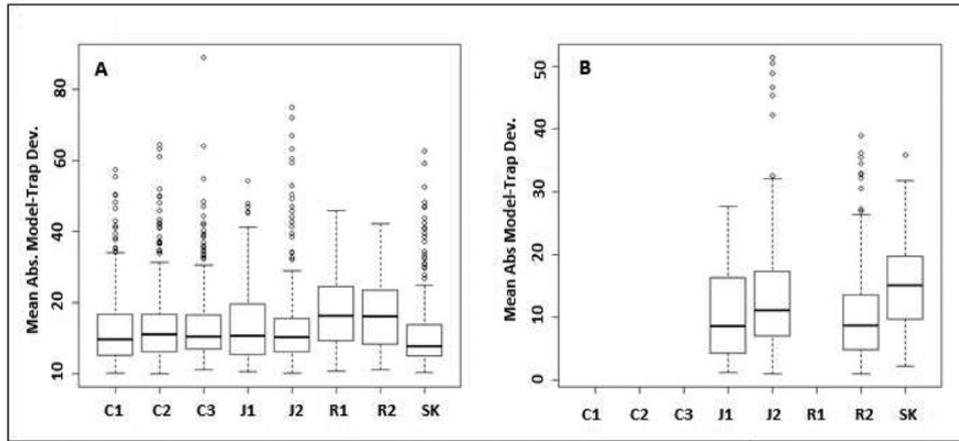
Fig. 3. The two panels represent the mean absolute deviations between the modeled and observed moth flight times based on whether the port was modeled using local phenology parameters (B), derived from the closest of the eight modeled populations, or all nonlocal populations (A). The use of local or nonlocal models did not affect the distribution of variance, indicating no improvement in model performance using local populations (based on the working definition of 'local').
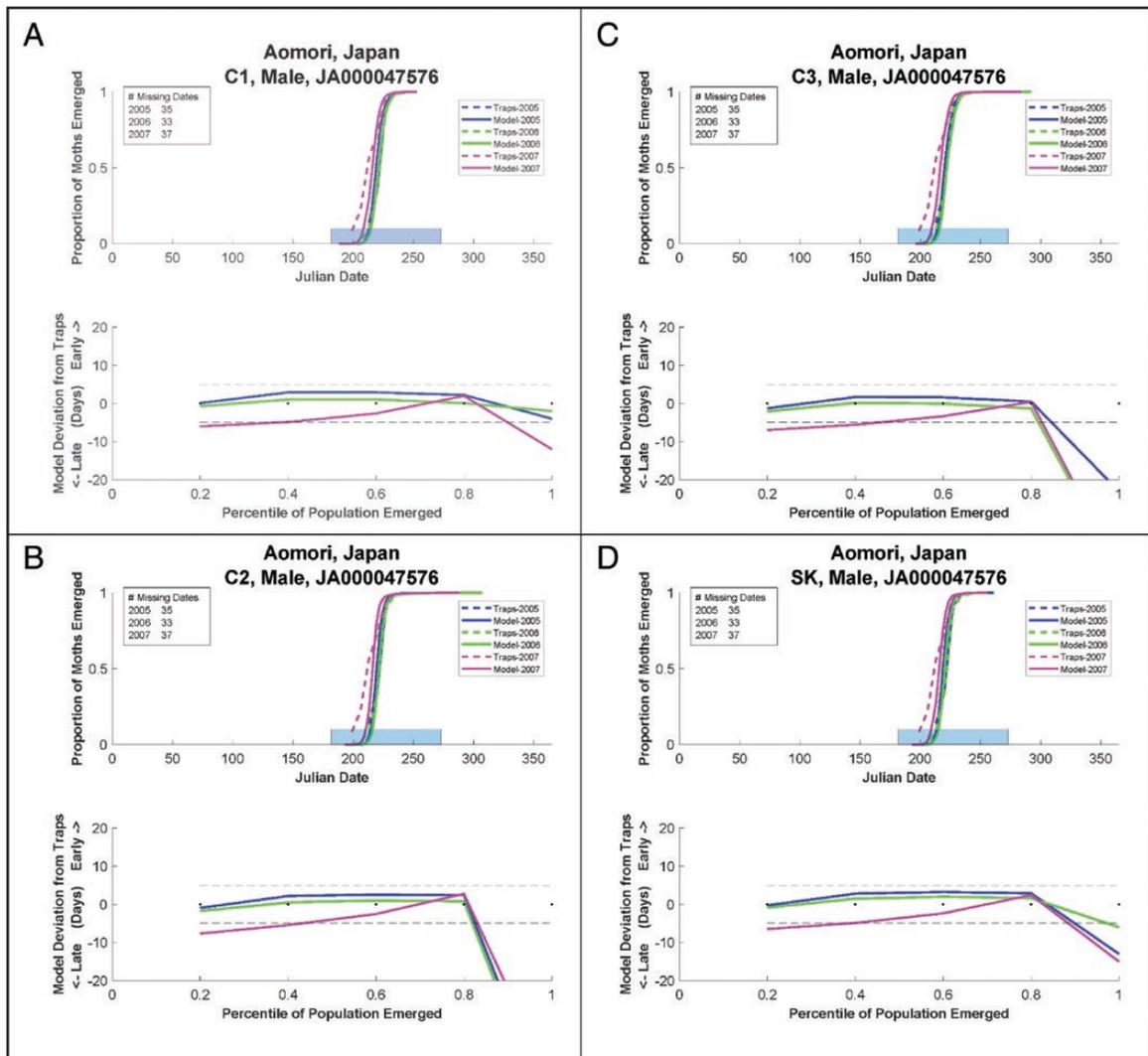
Fig. 4. Comparison of the flight times of males based on the model (solid lines) and trap data (dashed lines) for each of the 3 yr for which trap data were available for Aomori, Japan, for each of the eight population-based phenology models. The shaded box along the x-axis indicates the NAPPO-designated high-risk period.
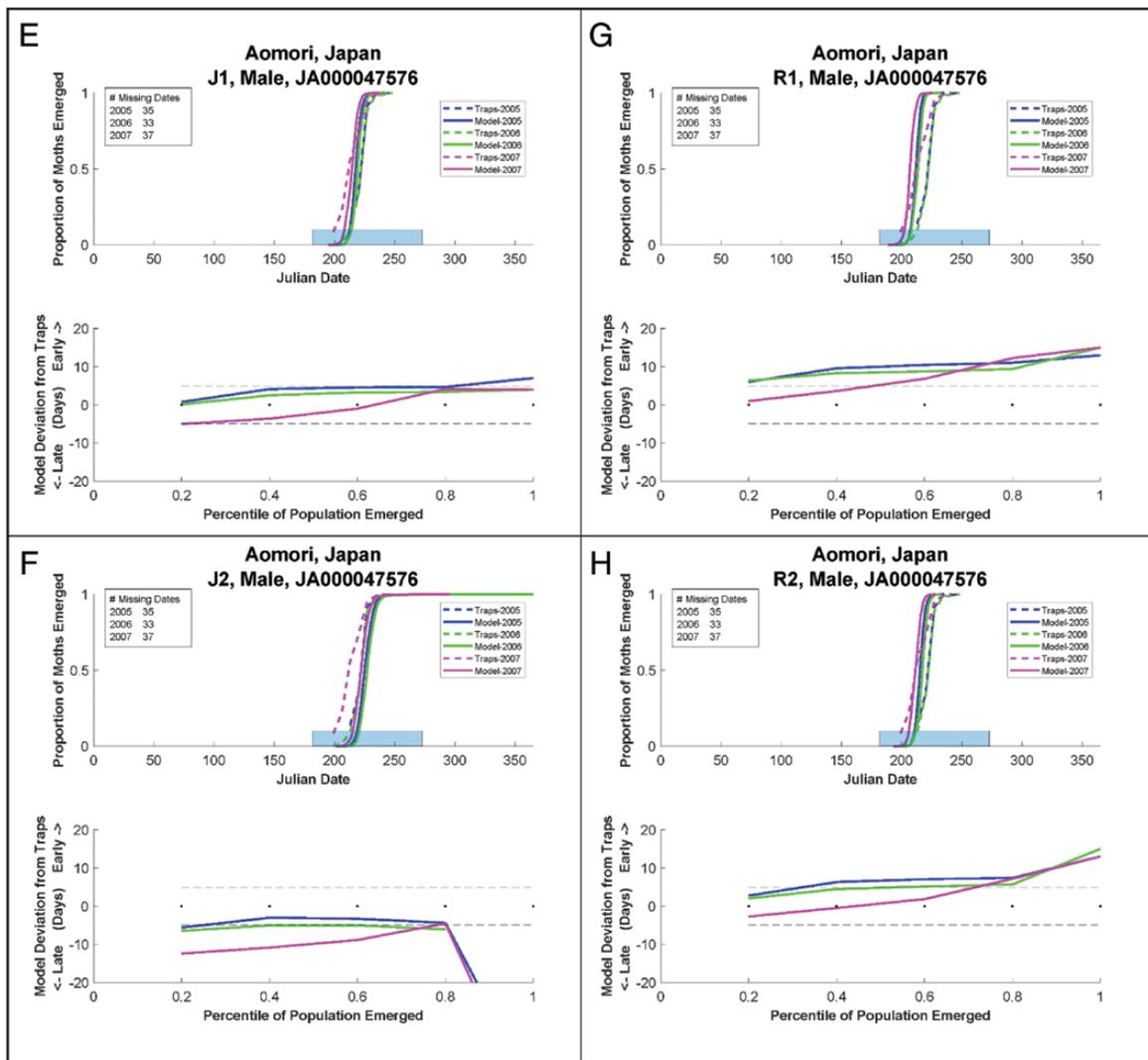
Fig. 4. Continued

was run for all 173 port–years. To standardize time steps and facilitate the comparison of simulated and observed patterns of moth flight, the proportion of the simulated emerged adult population was calculated at 2% increments and trap data were resampled at 2% intervals using linear interpolation of trap records. Deviations (measured in days) between the simulated and observed values were calculated by subtracting the date for each percentile increment in the simulated data set from the date for the corresponding percentile increment in the observed data. The result provides an estimation of the direction (positive or negative, i.e., early or late) and magnitude of error in the predicted timing of moth flight. The mean absolute deviation was calculated for each sex-population-port–year for an overall (nondirectional) estimate of model deviance from observed flight. For some graphical representations, mean absolute deviations were categorized based on whether the mean value was ≤5 d. The 5-d threshold was selected arbitrarily to provide a consistent criterion to graphically represent a snapshot of the variation among populations and ports. Statistical comparison among the distribution of the population/port/year mean absolute deviations within and among strains and sexes was determined using a Kolmogorov–Smirnov test (ks.test in R, R v3.5.3, 20 December 2018, R Foundation for Statistical Computing).

To assess the relative importance of using local Asian gypsy moth phenology models in a port, population–port–year output data sets were categorized based on whether the population used to parameterize the phenology model represented a local moth population. A port was assigned a local moth population based on its proximity to the closest location where moth populations were sampled (Table 2). Population–port combinations that were not based on these pairings were considered nonlocal. The comparison of overall error between local and nonlocal phenology models was made comparing the distributions of mean absolute deviations between the local and nonlocal model–port pairs using a Kolmogorov–Smirnov test as described previously.

To assess bias in both the magnitude and direction of deviations between the simulated and observed patterns of moth flight, port- and population-specific simulations were assessed graphically as recommended by Elandt-Johnson and Johnson (1980) and described by Logan et al. (1991). Example ports that demonstrate various types of model fit are provided here to facilitate discussion; the full set of 752 population–port–sex model output graphs is available in Supp Data S3 (online only).

Results

Variation among Population-Specific Asian Gypsy Moth Phenology Models

When applied to the same (full) set of port–years, the eight population-specific phenology models produce significantly different patterns of simulated flight times, as indicated by significant variation in the distribution of mean absolute deviations (nondirectional error) between simulated and trap data among the models. These differences are significant whether the sexes are pooled ($D = 0.6652$, $P < 0.00001$) or assessed separately (female moths: $D = 0.6252$, $P < 0.00001$, male moths: $D = 0.7052$, $P < 0.00001$; Fig. 2A–C). These differences suggest that the variation in phenological requirements observed by Limbu et al. (2017) translates to differences in predicted phenology when applied to locations where the moth is native. Although the variation among strains is significant, representation of the data in box-and-whisker plots can tend to emphasize the outlying points. For some ports, none of the phenology models provided reasonable estimates of flight time, resulting in the numerous points

shown above the 95th percentile in Fig. 2A–C. To assess patterns without this variance data representing port–years for which predicted flight times might be considered reasonable (i.e., the mean absolute deviation between the simulated and observed moth flight was 5 d or less) are shown in Fig. 2D. As the figure demonstrates, when applied generally to each of the port–years, the eight phenology models based on different populations were highly variable in the frequency with which they predicted the overall flight season within the 5-d cutoff.

Local versus Nonlocal Moth Populations

Although the eight models produced variable estimates of flight time among the ports, the use of local phenology models (i.e., based on the nearest moth population for which phenology parameters are available) did not increase the overall fit between the predicted and observed patterns of moth flight ($D = 0.0605$, $P < 0.218$; Fig. 3A and B). Combined, these data suggest that although the eight models produce variable estimates of flight, the use of a local model does not generally improve the fit of the model.
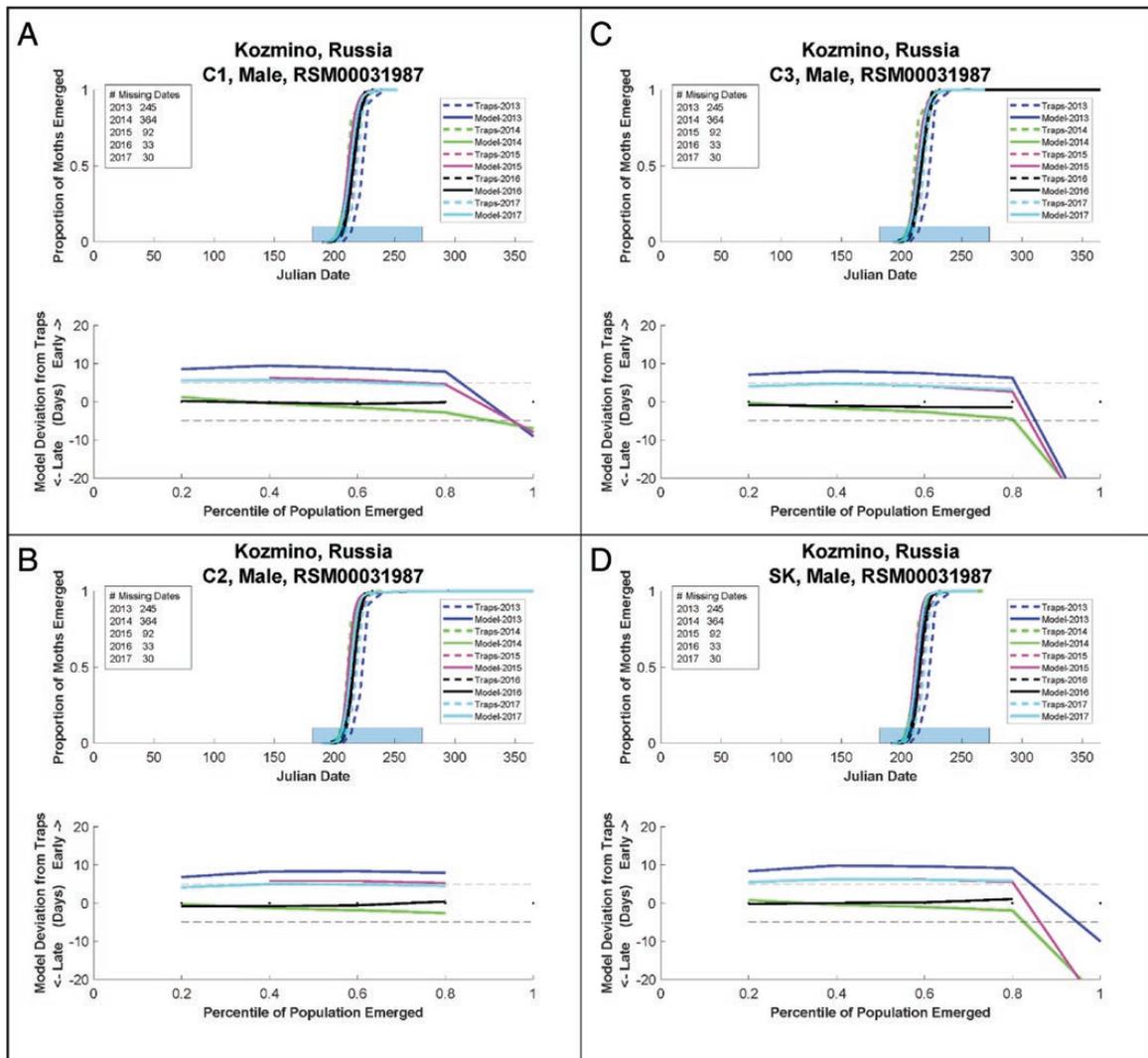
Fig. 5. Comparison of the flight times of males based on the model (solid lines) and trap data (dashed lines) for each of the 5 yr for which trap data were available for Kozmino, Russia, using each of the eight population-based phenology models. Note that there is variation in accuracy among the eight models and the deviations tend to indicate some models run too early. Also, note the variation in model fit among years, with 2014 and 2016 providing consistently better results. The shaded box along the x-axis indicates the NAPPO-designated high-risk period.
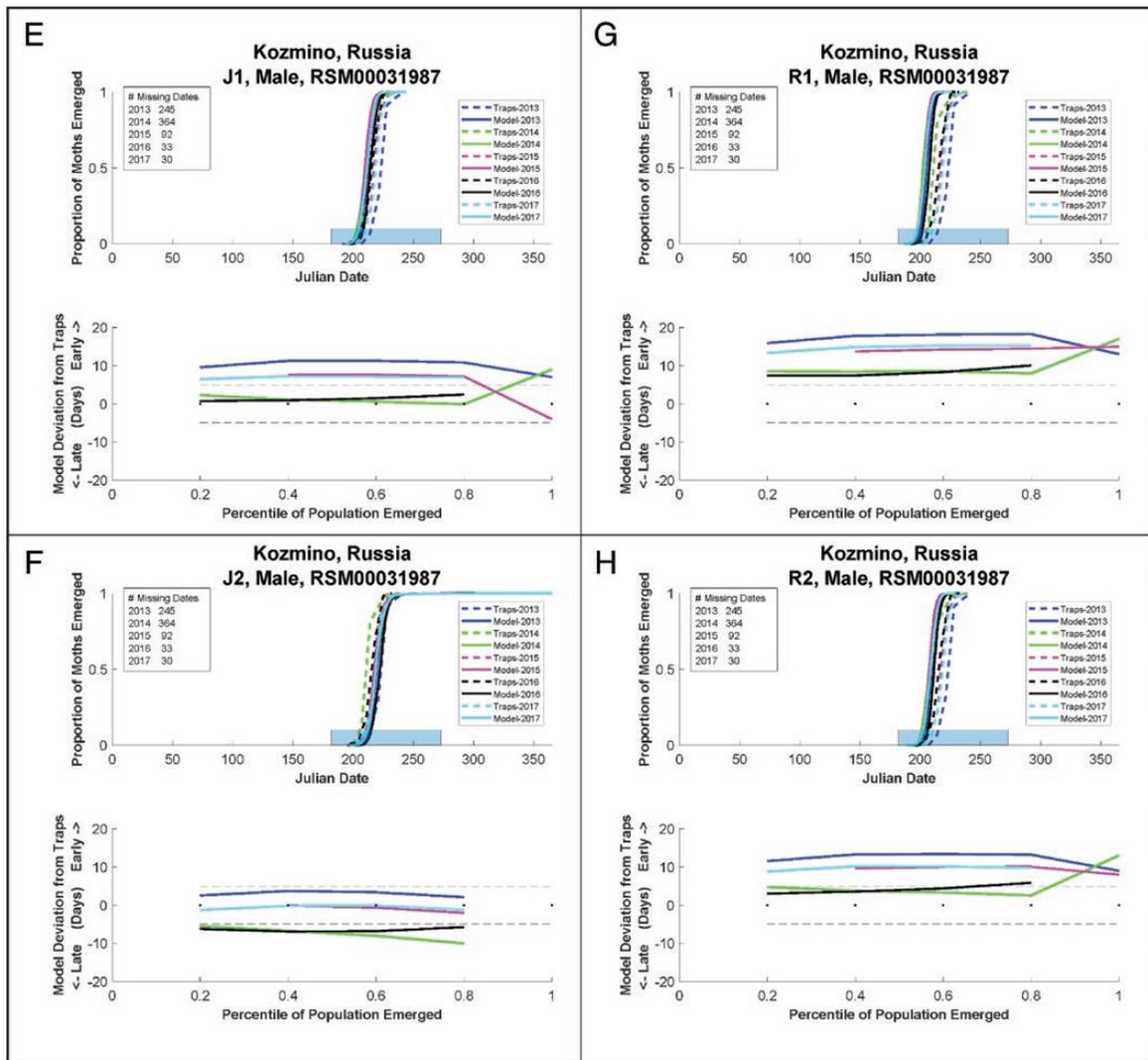
Fig. 5. Continued

Variation in the Suitability of the Models among Locations and Years

A comparison of the eight male phenology models with the flight timing documented by the males collected in traps shows there is tremendous variability in the fit of the models among populations, ports, and years. Generally, the results for ports can be placed in three categories. First, within some ports the simulated flight times correspond well with the trap data across the range of population-based models. An example is shown by Aomori, Japan (Fig. 4A–H) where model output based on population parameters from China, Japan, and the Republic of Korea performed well across all 3 yr, with slightly reduced fits for phenology models based on populations from Russia (Fig. 4G and H). The agreement between the simulation and the trap data suggests that for this location, the larva-to-adult model works well, the inclusion of an egg-diapause model may not be necessary, and the models have potential application for use in predicting the timing of second instars.

A second general category of ports is exemplified by Kozmino, Russia (Fig. 5A–H). For these ports, the fit of the models is variable both among the eight sets of population parameters and among years within the port. As the graph shows, the general predicted flight times for J1, C1, C2, and C3 are relatively consistent, if slightly early

(Fig. 5A–D). However, the predicted flight times for both R1 and R2 (Fig. 5G, F, and H, phenology models based on Russian populations of the gypsy moth) predict dates that substantially pre-date the observed patterns of moth flight documented by the traps. Also, there is substantial variation in the fit of the model among years. The predicted flight times in Kozmino based on the phenology parameters from the Republic of Korea were accurate in 2014 and 2016, but were early in 2013, 2015, and 2017. This suggests that although a given population model may generally fit a port, individual years may be divergent.

Finally, there are locations such as Busan, Republic of Korea (shown in Fig. 6A–H) where none of the population phenology models provide reasonable predictions of moth flight. Ports with these substantial errors can express errors in both directions, with predictions greatly preceding or lagging periods of trap-documented flight.

Discussion

Since the first documented detection of the Asian gypsy moth in North America in 1991 (Bogdanowicz et al. 1993), increased effort has been directed toward assessing and mitigating the risk of
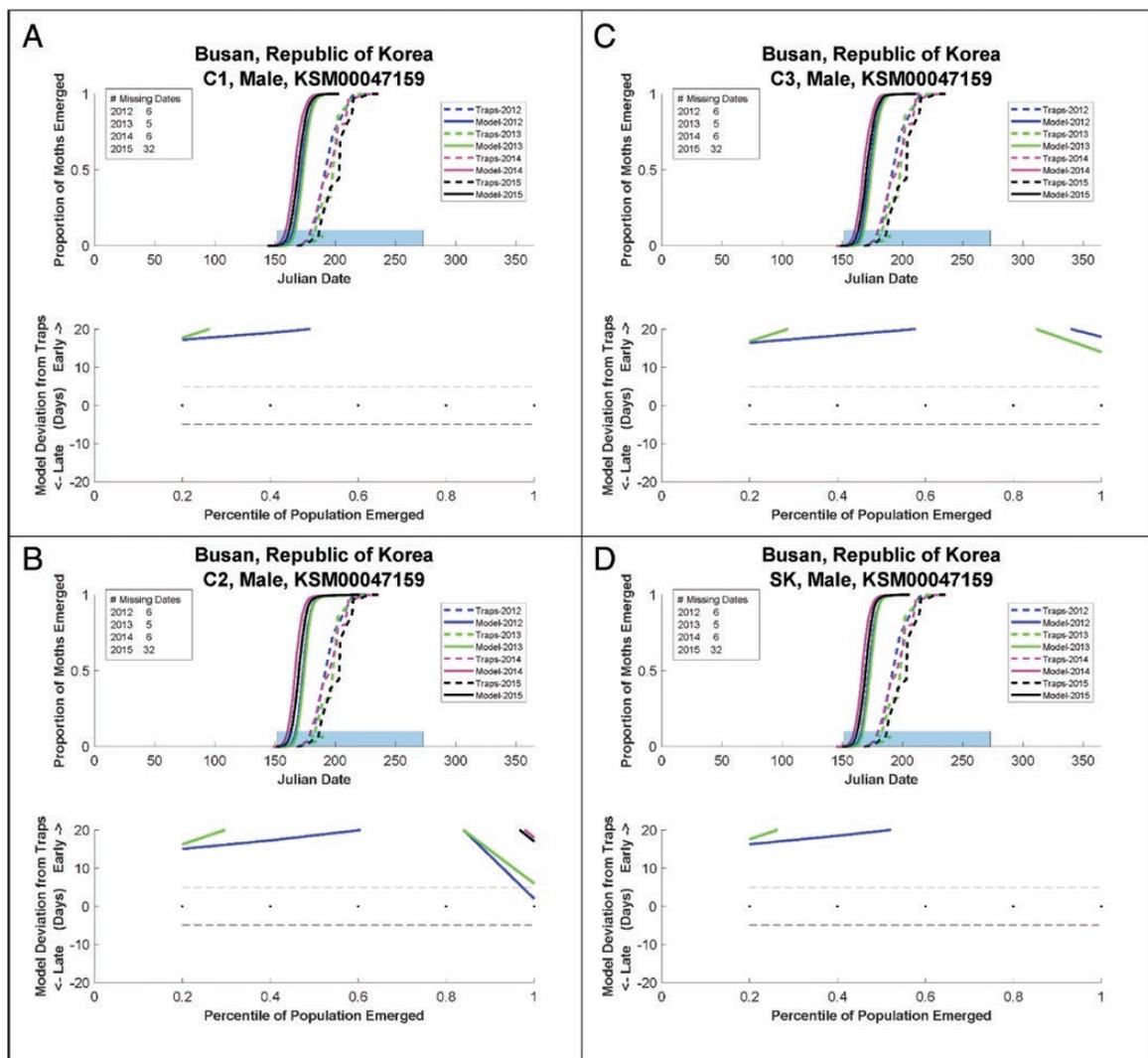
Fig. 6. For some ports, none of the phenology models generated suitable predictions of moth flight (Busan, Republic of Korea port shown as an example). These errors may be the result of ports with moth populations that are not represented by any of the eight populations, the result of weather stations with erroneous data, or from model failure based on incomplete or missing components such as egg development. Stations were not replaced with other (more distant) weather stations to improve fit to avoid 'fishing' for model improvement, though further analyses are clearly merited. The shaded box along the x-axis indicates the NAPPO-designated high-risk period.

introducing this moth to new landscapes. A key component of these efforts is the need to assess when cargo and vessels in source ports in East Asia may become infested with egg masses. The phenology of the insect structures much of this risk; studies by Gray (2010, 2016) and Magarey et al. (2015) have provided tools to assess this risk, but have been limited by their use of phenology parameters based on the European gypsy moth. The analyses described here represent the development of phenology models based on the Asian gypsy moth, assessments of the variation in phenological requirements among subspecies and populations of the Asian gypsy moth, and the potential impact this variation may have on the utility of predicting moth life stages across a broad range of international ports in East Asia. Although much work on this system remains to be done, the results demonstrate several key findings.

First, the models described here show that the variation in phenological requirements and parameters among populations and subspecies of the Asian gypsy moth, as documented by Limbu et al. (2017), translates to variation in the suitability and accuracy of phenology models across varied ports in East Asia. These variable model fits

suggest that additional work may be needed to assess the use of European gypsy moth models to predict risk for strains of the Asian gypsy moth (Pitt et al. 2007; Gray 2010, 2016; Magarey et al. 2015). These analyses also show that variation in phenological parameters between male and female moths are significant across a range of locations. However, for those port–population combinations in which male phenology models reasonably predict periods of male flight, the corresponding female phenology models may have utility in more precisely predicting the timing of oviposition (the activity that poses risk). Whether these gender-based differences in estimated flight time are relevant to management strategies remains to be determined, but given the costs involved in inspecting ships and cargo, refinements in the requirements for inspections yield cost savings or may further mitigate risk.

The variation among the eight population-based phenology models suggests the use of the appropriate population–port pairing has the potential to improve model performance in a given port. However, these results also raise a number of new questions. First, these analyses suggest the use of local population models did not
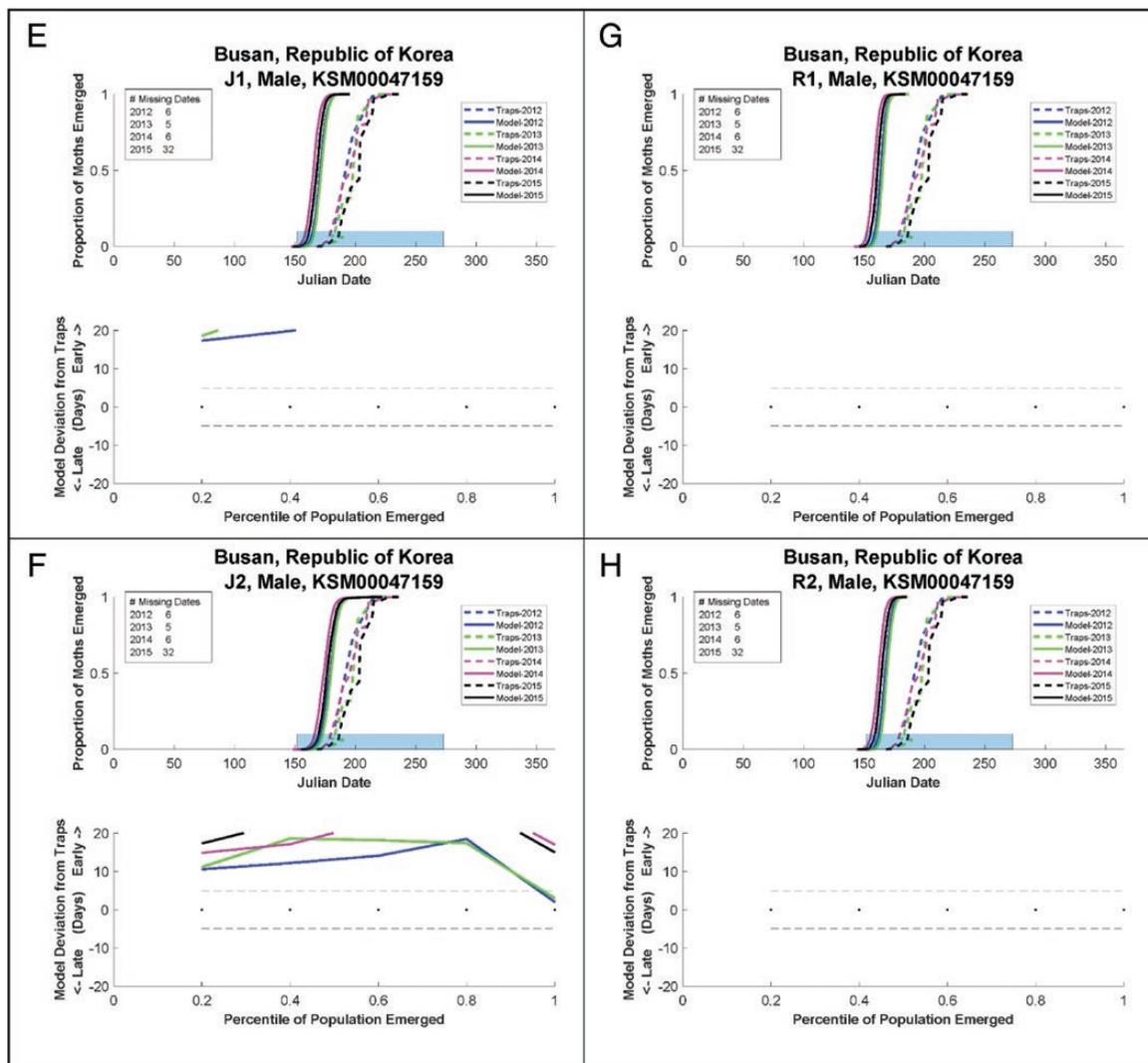
Fig. 6. Continued

generally improve model performance. The failure of the local models to improve the fit between the predicted and observed male moth flight periods may be the result of several factors, including a disconnect between the scale and distribution of sampled moth populations and the distribution of ports evaluated. If the landscape includes populations that have not been sampled, and the sizes and distributions of moth populations are unevenly distributed across the landscape, the population defined as local in these analyses may not represent the actual local population of moths in a given port. Similarly, variation in the range occupied by populations may explain why some ports were well suited to many of the models (if the population in the port is broadly distributed), whereas in some ports, none of the models fit well, perhaps indicating the port hosts a highly localized moth population that has not been parameterized.

Some locations (Aomori, Japan for example) suggest the use of a larva-to-adult model (which omits the complexities and variation associated with egg development) may produce acceptable results. However, ports such as Kozmino, Russia, suggest the suitability of omitting the egg stage may not be generalizable among populations and ports. As the panels in Fig. 5 show, the models based on parameters from populations in China (C1, C2, and C2), Japan (J1 and J2), and the Republic of Korea (SK) were effective in predicting the timing of male moth flight, suggesting they are capturing (or correlating with) the biology of the moths in this location (Fig. 5A–F).

However, the predictions for flight based on Russian moth populations (R1 and R2, which are closer to Kozmino than the other populations) predicted flight times that were too early (Fig. 5G and H). Observations by Limbu et al. (2017) and M. A. Keena (unpublished data) have shown that moths from the R1 population (where conditions are generally cooler) tend to develop more rapidly and at lower temperatures. Moths in this population also go through fewer instars and R1 is the only studied Asian gypsy moth population known to pupate after only four instars. If the resident moth populations in Kozmino have the same behavior as the more cold-adapted R1 population, it is possible that the early prediction provided by the Russia population models is the result of a missing component (such as the egg stage), which might otherwise delay the development of first instars. If this is the case, then by extension the correct prediction of flight periods given by the other population models for this location may be the result of a shift toward early flight resulting from a missing egg stage, balanced by a shift toward later flight resulting from the application of a more warm-adapted population to a cold temperature regime, though this is largely conjecture. Currently, the available data do not provide a direct way to test these possibilities. However, it is worth noting that these counter-balancing errors (if they are occurring) are not consistent across ports. Evidence of this is provided by ports such as Aomori for which estimated flight times were reasonable across the range of moth population models.

In addition to providing a way to evaluate the need to include more complex processes such as egg development, these models may provide alternative methods to quantify or estimate the timing of additional life stages, such as egg hatch, or correlates (such as temperature) with these life stages. For example, if the starting point of the phenology model (when first-instar larvae can begin development) is shifted forward in time until predicted flight matches observed patterns, the modified start date for the model may suggest a time when eggs have hatched for a given year and location. Assessing the years and locations as a group may provide some ways to reverse-engineer the timing of egg hatch. Similarly, this approach may allow the estimation of life-history events such as the initiation of second-instar development, when management tools such as biopesticides may be applied to reduce moth populations (Reardon et al. 1994).

Overall, these models suggest that the approach being used here has utility, but that additional work is needed to identify the drivers of variation among ports, populations, and years. As broader-scale observational data sets and information networks such as those hosted by the USA National Phenology Network (usanpn.org) continue to grow, the broad types and distributions of data needed to assess the effects of complex landscape processes on the phenology of species may continue to improve. However, in the absence of these data sets, models will continue to depend on readily gathered metrics such as temperature.

Supplementary Data

Supplementary data are available at *Annals of the Entomological Society of America* online.

Acknowledgments

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