

# Hitchhikers on trade routes: A phenology model estimates the probabilities of gypsy moth introduction and establishment

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**Abstract.** As global trade increases so too does the probability of introduction of alien species to new locations. Estimating the probability of an alien species introduction and establishment following introduction is a necessary step in risk estimation (probability of an event times the consequences, in the currency of choice, of the event should it occur); risk estimation is a valuable tool for reducing the risk of biological invasion with limited resources. The Asian gypsy moth, *Lymantria dispar* (L.), is a pest species whose consequence of introduction and establishment in North America and New Zealand warrants over US\$2 million per year in surveillance expenditure. This work describes the development of a two-dimensional phenology model (GLS-2d) that simulates insect development from source to destination and estimates: (1) the probability of introduction from the proportion of the source population that would achieve the next developmental stage at the destination and (2) the probability of establishment from the proportion of the introduced population that survives until a stable life cycle is reached at the destination. The effect of shipping schedule on the probabilities of introduction and establishment was examined by varying the departure date from 1 January to 25 December by weekly increments. The effect of port efficiency was examined by varying the length of time that invasion vectors (shipping containers and ship) were available for infection. The application of GLS-2d is demonstrated using three common marine trade routes (to Auckland, New Zealand, from Kobe, Japan, and to Vancouver, Canada, from Kobe and from Vladivostok, Russia).

**Key words:** alien species; Auckland, New Zealand; biological invasion; gypsy moth (*Lymantria dispar*); introduced species; invasion vector; Kobe, Japan; pest establishment; risk analysis; risk estimation; Vancouver, Canada; Vladivostok, Russia.

## INTRODUCTION

Biological invasion is generally considered to consist of three stages (Shigesada and Kawasaki 1997, Tatem et al. 2006, Liebhold and Tobin 2008): dispersal (i.e., arrival or introduction at a new location), establishment, and spread. Risk is defined (Hopper 1993, Schmoldt 2001) as the product of the probability of an event occurring and the consequence(s) of the event should it occur. The risk of biological invasion is then the probability of introduction times the probability of establishment given an introduction times the probability of spread given the joint probability of introduction and establishment times the consequences given the joint probability of introduction, establishment, and spread [ $p(I) \times p(E|I) \times p(S|E|I) \times \text{consequences}$ ]. Historical increases in the risk of biological invasion have been due almost exclusively to increases in the probability of introduction that accompanied increases in travel and trade. This paper examines how shipping schedules can affect the risk of biological invasion by altering the

probability of introduction and establishment of an alien insect pest.

Estimating the probabilities of introduction and establishment of an alien species in a given locale is of interest for a number of reasons. Where either the probability of introduction or establishment is near zero, the associated regulatory activities, such as survey and inspection of introduction pathways, and eradication efforts (in the event of introduction), can be minimal. Where the probabilities of introduction and establishment are both high, greater expenditure of human and financial resources is recommended to limit (or prevent) introduction and to eradicate introduced populations before spread occurs. Establishing priorities based on risk is an effective way of assigning limited resources.

One strategy for estimating the probability of establishment, given an introduction [i.e., the conditional probability  $p(E|I)$ ], employs climate-matching analyses (Walter et al. 1975) to compare the climatic conditions in the natural host range with the climatic conditions at the point of potential establishment. Climate matching has been used to assess the probability of establishment of many organisms, e.g., the Old World screw-worm (*Chrysomya bezziana*) (Sutherst et al. 1989), the Mediterranean fruit fly (*Ceratitis capitata*

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(Wiedemann)), and the Colorado potato beetle (*Leptinotarsa decemlineata* (Say)) in New Zealand (Worner 1988), and the gypsy moth (*Lymantria dispar* (L.)) in Florida (Allen et al. 1993). Climate matching relies on general inferences regarding an organism's response to climate and is useful when too little biological information exists to build a detailed model (Sutherst and Maywald 1985).

When an accurate and geographically robust model of insect phenology exists, it can reasonably be assumed that such a model will give a more accurate estimate of  $p(E|I)$  than climate matching. For poikilothermic insects, a phenology model simulates the developmental (ontogenetic) response of the insect to temperature. Thus, a phenology model can directly assess one critical criterion for establishment: the degree to which the local climate produces seasonality in the insect life cycle. Seasonality is the predictable "occurrence of [a life stage event] within a definite limited period or periods of the astronomic (solar, calendar) year" (Lieth 1974:5). For temperate insects this implies that emergence of a feeding stage is coincident with presence of suitable host material, that winter will be passed in a cold-hardy stage, and that these events will coincide sufficiently each year for the continued survival of the population.

The level of confidence that should be placed on estimates of  $p(E|I)$  derived from a phenology model is directly related to the expected accuracy of model predictions. The expected accuracy, measured on a large landscape scale, is a function of the geographic robustness (i.e., the ability to perform satisfactorily over a broad, and climatically variable, geographic range) of the model. Unfortunately, very few insect phenology models are known to exhibit satisfactory geographic robustness. At least one exception is the composite gypsy moth life stage (GLS) model (Gray 2004), which uses a sequential three-phase paradigm (Gray et al. 1991, 1995, 2001) to model egg development and hatch, arguably the most critical life stage event for establishing seasonality. The development of subsequent early larval stages is simulated by the model of Logan et al. (1991); development of late larval stages and adult stages are simulated by the model of Sheehan (1992). The GLS (gypsy moth life stage, or Gray/Logan/Sheehan) model does not rely on a user-supplied starting date, a date that is generally unknown at potential introduction locations, commonly required by phenology models. Instead GLS establishes a likely oviposition period in each location by a stabilization process using local temperatures (Gray 2004). Alternatively, a user can initiate a GLS simulation with either oviposition or hatch by stipulating one or several arbitrary dates. Population variability in developmental rate is modeled independently in each egg phase and each subsequent life stage. Stochasticity is through the random selection of years of temperature data for the stabilization process and, if desired, through a random selection and ordering of years in multiyear simulations. The GLS model has been

used to estimate  $p(E|I)$  of the gypsy moth in western Canada (Régnière and Nealis 2002), Utah (Logan et al. 2006), and North America (Gray 2004). A recent reformulation of the age-dependent postdiapause process leading to egg hatch in GLS resulted in significant improvements to model predictions (Gray 2009). The modifications caused simulated egg hatch to be advanced in some cases, but retarded in others; it caused the hatch period to be shortened in some cases, but unchanged in others. Model error was reduced substantially in all test sites in Virginia, New Brunswick, and British Columbia (Gray 2009).

The gypsy moth was accidentally released in Medford, Massachusetts, USA, in 1868 or 1869 (Liebhold et al. 1989) and has since expanded its range south, north, and west. Defoliating populations are established from North Carolina, USA, to New Brunswick, Canada, and west to Michigan, USA, and Ontario, Canada. Isolated populations have been detected in Missouri, Utah, Oregon, and Washington, USA, and British Columbia, Canada. Natural dispersal of the flightless-female strain of gypsy moth in North America is predominantly by wind dispersal of first-instar neonate larvae and may be <30 m/yr (Mason and McManus 1981, Weseloh 1997). Longer distance dispersal is via human movement of objects on which females commonly lay their egg masses (Liebhold et al. 1992, Sharov and Liebhold 1998).

The risk of gypsy moth invasion became a considerable concern to resource managers in New Zealand in the early 1990s when egg masses were discovered in shipping containers arriving from the Far East (Japan and Korea). Approximately US\$3.8 million was expended in 2003–2005 on the eradication of an Asian gypsy moth population in Hamilton (Biosecurity New Zealand 2007), 50 km from Auckland. Annual surveillance costs (approximately \$261 000) are paid by a levy on sea container and used-car imports (Anonymous 2008). Pitt et al. (2007) used the GLS model (although they incorrectly called it the "GMLS" model) to investigate  $p(E|I)$  of the Asian, female, flighted strain of gypsy moth in New Zealand. The risk of Asian gypsy moth invasion from Japan, Korea, and the Russian Far East is of similar concern to regulators in North America. More than \$4.3 million was expended in 1992 to eradicate a population on southern Vancouver Island, Canada (L. Humble, *personal communication*). In 2008, an unprecedented 10 commercial vessels were ordered back into international waters from Pacific ports (United States and Canada) because of their significant infestation levels (Canadian Food Inspection Agency and U.S. Department of Agriculture 2009). The U.S. government spends approximately \$1.3 million/year in surveillance activities involving the Asian gypsy moth (W. Fussell, *personal communication*). Canada spends approximately \$0.4 million/year in western Canada (N. Kummen, *personal communication*).

Despite the importance of long-range trade routes in the introduction of gypsy moth, the spatiotemporal variability in weather and its effect on gypsy moth phenology has never been a consideration in estimating  $p(I)$  or  $p(E|I)$ . That is to say: the degree to which pre-departure phenological development at the source plus phenological development en route plus post-arrival development at the destination influences  $p(I)$  and/or  $p(E|I)$  has not been considered in the invasion risk calculations. The pronounced spatiotemporal changes in weather during transoceanic transport have the potential to disrupt the normal phenological development and could be a significant factor in  $p(I)$  and  $p(E|I)$ .

This paper describes a two-dimensional extension of the GLS model (GLS-2d) that incorporates the transit route and schedule and temperature regimes at the source, en route, and at the destination into the phenological simulation. This two-dimensional phenology model provides a more reliable estimate of  $p(I)$  and of  $p(E|I)$  of an invasive insect that is commonly introduced by the long-range transport of egg masses.

#### METHODS

##### *Evaluating gypsy moth phenology models: GLS 2004 or GLS 2009*

Pitt et al. (2007) assumed, in the absence of information to the contrary, that GLS model parameters (that had been validated only for the European strain) would give accurate developmental estimates for the Asian strain in which they were interested. As a first step, this assumption was tested here by comparing the weekly observations of male moth capture in pheromone-baited traps in 2006 at Kishiwada, Japan (34.461° N, 135.371° E; 15 m elevation) with GLS-simulated male moth frequencies using temperature data from the nearest weather station (Kobe, Japan; 34.680° N; 135.180° E; 59 m elevation). Simulations used either the same GLS parameters as Pitt et al. (2007), (described by Gray [2004] and hereafter called GLS 2004) or used the newer parameters described by Gray (2009) (hereafter called GLS 2009). In both cases, the simulations were initiated by the oviposition stabilization process and then used daily weather station data to simulate five generations (2001–2006) culminating in oviposition in 2006. Ten fully independent simulations (i.e., independent random years for the stabilization process) were conducted by GLS 2004 and GLS 2009, and the simulated daily frequencies of male moths were compared visually with the observed pheromone trap captures of male moths. The GLS 2009 parameters were judged superior (see *Results*) and were used for the remainder of the simulations described here with GLS-2d.

##### *Probabilities of introduction and establishment with GLS-2d: an extension to GLS 2009*

In the simulations described here, GLS-2d was initiated by a modification of the stabilization process

described by Gray (2004). Ten simulated, equal-sized egg cohorts were oviposited at 35-d intervals from 10 January to 21 November in two ports of origin: Kobe, Japan, and Vladivostok, Russia (43.114° N, 131.902° E; 20 m elevation). Both ports are considered by the Canadian Food Inspection Agency (CFIA) and the United States Department of Agriculture, Animal and Plant Health Inspection Agency (USDA-APHIS) to contribute to a “high” risk of introduction to North America. This overly protracted oviposition period maximizes the probability that at least some of the eggs of this first stabilization generation will hatch and some larvae will reach the adult stage and complete oviposition in each origin. After each stabilization generation, the daily numbers of oviposited eggs were increased by a common factor to replenish the stabilization population to its starting size to prevent the population from “dying out” during stabilization, while maintaining the temporal distribution of oviposition. If no egg of the stabilization population was successful in completing its life cycle and ovipositing the next generation, the stabilization population was relaunched with the last successful oviposition pattern. Gray (2004) found that the oviposition pattern stabilized within 3–7 generations. Therefore, the oviposition pattern of the seventh successful stabilization generation was used to initiate development of the simulated population at the origin. If five successive years failed to result in a complete life cycle, the stabilization process was relaunched with the 10 January to 21 November oviposition pattern and the count of successful generations was returned to zero, until a maximum of 25 years had been attempted. Yearly temperatures were chosen at random from the available data for each origin for stabilization.

An extension to GLS 2009 (GLS-2d) simulates gypsy moth phenology as the population is transported from its origin to a potential point of introduction. Transit routes were described between Kobe, Japan, and Auckland, New Zealand (36.835° S, 174.755° W; 31 m elevation), between Kobe and Vancouver, British Columbia, Canada (49.30° N, 237.750° W; 3 m elevation), and between Vladivostok, Russia, and Vancouver. Transit times of 12 d (Kobe–Auckland and Kobe–Vancouver) and 11 d (Vladivostok–Vancouver) were assumed after examining published advertisements for shipping companies. Equally spaced, daily waypoints were identified along the shortest route between origin and destination. For each origin, waypoint, and destination, GLS-2d used the weather records from the nearest location in a weather database (see *Weather database*, below). The effect of departure date on  $p(I)$  and  $p(E|I)$  in each destination was examined by allowing GLS-2d to establish (by the stabilization process) an oviposition profile (frequency vs. day) of the  $F_0$  generation at the origin. Oviposition occurs on cargo containers and a ship when they are in a port of origin, so these assumptions were made regarding the arrival of containers and ships

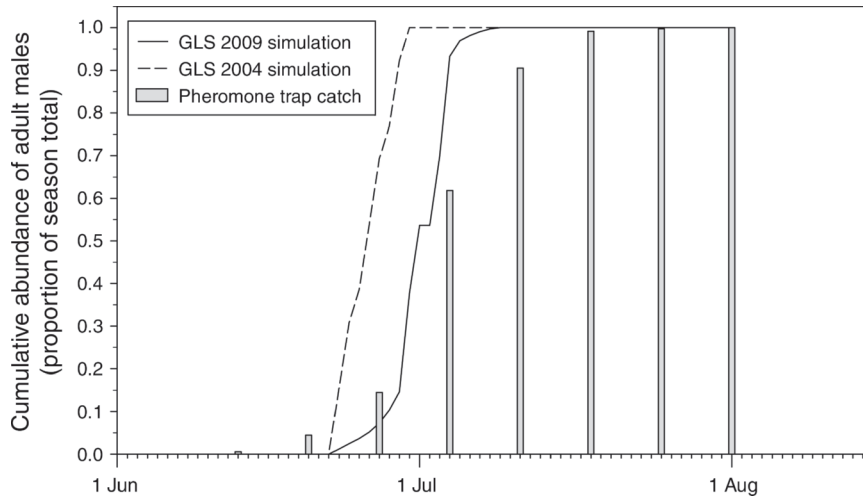


FIG. 1. Observed weekly cumulative male adult gypsy moth (*Lymantria dispar*) abundance and simulated cumulative abundances from the gypsy moth life stage models GLS 2004 and GLS 2009. The models differ in their use of a linear (GLS 2004) or a nonlinear (GLS 2009) temperature-dependent developmental response at postdiapause initiation.

at the origin: (1) containers arrive over a 6-d period; (2) the last container arrives 6 d before the ship; (3) ship departs 6 d after arrival; and (4) container surfaces can hold twice the number of oviposited egg masses as a ship. The development of the  $F_0$  generation was simulated at the origin until departure date, then development of egg masses oviposited on containers and ship was simulated for 1 d at each waypoint of the transit route and thereafter at the destination. The oviposition profile of  $F_{i+1}$  (at the destination) was defined by the emergence profile (frequency vs. day) of adult females of  $F_i$ , thereby maintaining the full extent of phenological variability in the simulation. Fifty-one departure dates at 7-d intervals were tested, and 25 fully independent simulations using a random selection of yearly temperature data were conducted for each departure date and each transit route. Daily frequencies and cumulative frequencies of each immature life stage and of male and female moths were recorded by GLS-2d.

The proportion of the  $F_0$  eggs oviposited at the origin that subsequently hatched at the destination was calculated for each simulation of each departure date. The  $p(I)$  for each departure date was calculated as the mean of the 25 hatched-from-oviposited proportions. When eggs hatched at the destination, the simulation continued for seven additional generations (hatching eggs to hatching eggs), and the geometric mean of intergenerational survival

$$\left( \prod_{i=1}^7 \frac{y_i}{y_{i-1}} \right)^{1/7}$$

was calculated for each simulation of each departure date. The  $p(E|I)$  for each departure date was calculated as the mean of the geometric averages from the departure date. Seven generations were used for the

calculation of  $p(E|I)$  because a stabilized life cycle pattern is usually achieved within seven generations (Gray 2004).

#### Weather databases

Daily (1971–2000) weather records (minimum and maximum temperatures) were obtained for Kobe, Vladivostok, and Vancouver from the Global Historical Climatology Network database (EarthInfo 2009). Daily weather records were obtained for maritime locations at  $\sim 2.8^\circ$  spatial resolution from simulations of the Canadian Global Circulation Model version 3 (Canadian Centre for Climate Modelling and Analysis 2008). Daily weather values were obtained for Auckland from the New Zealand National Institute of Water and Atmospheric Research (2002).

#### RESULTS

##### Evaluating gypsy moth phenology models: GLS 2004 or GLS 2009

Although the final moth capture in Kobe did not occur until 1 August,  $>99\%$  of the total trap capture had occurred by 18 July. Therefore, I have used 13 June–18 July (36 d) as the approximate duration of male moth presence. Both models (GLS 2004 and GLS 2009) underestimated the duration of male moth presence (Fig. 1); however, the predicted duration from GLS 2009 (17 d) was substantially more accurate than the predicted duration from GLS 2004 (8 d). The weekly observations of cumulative trap catch were also more accurately predicted by GLS 2009 than by GLS 2004. Therefore, parameters of GLS 2009 were deemed more accurate than those of GLS 2004 for simulating Asian gypsy moth phenology and were used for all GLS-2d simulations.



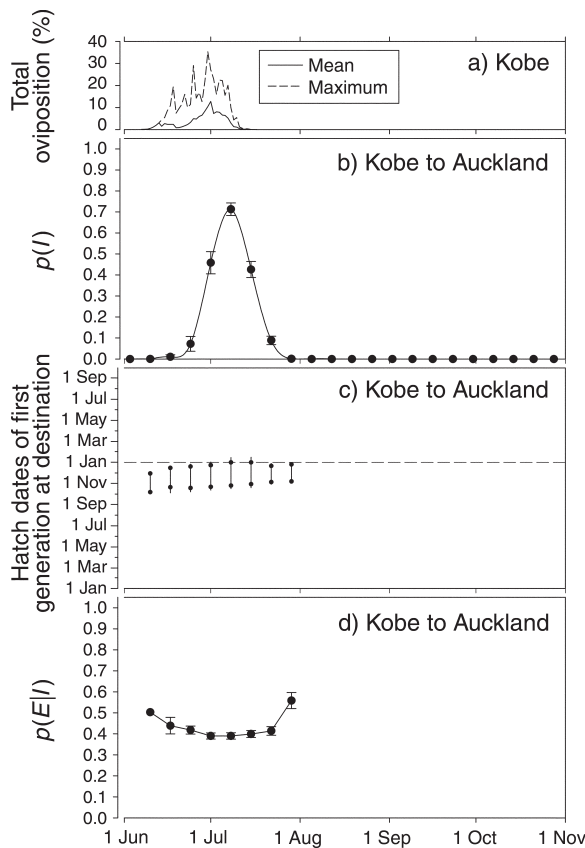


FIG. 2. (a) Daily gypsy moth oviposition frequency, as a percentage of season total, at Kobe, Japan, (b) probability of introduction [ $p(I)$ ; mean  $\pm$  SE], (c) first egg hatch period, and (d) probability of establishment given an introduction [ $p(E|I)$ ; mean  $\pm$  SE] in Auckland, New Zealand, under a best-case scenario. Minimum daily oviposition frequency in Kobe was most often zero and is not shown. In panel (c), mean days of first and last egg hatch in Auckland are shown by solid circles, and extremes are indicated by end points of vertical bars.

*Probabilities of introduction and establishment with GLS-2d*

Simulated oviposition occurred 7 June–15 July and 13 August–6 November in Kobe (Figs. 2a and 3a) and Vladivostok (Fig. 4a), respectively. There is a nonzero  $p(I)$  to Auckland and Vancouver for ships departing Kobe after commencement of egg oviposition and before 5 August and nonzero to Vancouver for ships departing Vladivostok after commencement of egg oviposition and before 14 October. The  $p(I)$  was  $0.034 \pm 0.018$  (mean  $\pm$  SE) for the 52 departure dates of the Kobe–Auckland and Kobe–Vancouver routes and  $0.017 \pm 0.008$  for the Vladivostok–Vancouver route. The  $p(I)$  was high ( $\geq 0.1$ ) for three and zero for 44 of the 52 weekly departure dates (all routes) (Figs. 2b, 3b, and 4b). When  $p(I) \geq 0.1$ , the duration of the hatch period of the first generation at the destination ( $F_0$ ) was  $64.3 \pm 1.3$  d,  $116.3 \pm 5.2$  d, and  $41.0 \pm 0.6$  d at Auckland, Vancouver (following transit

from Kobe), and Vancouver (following transit from Vladivostok), respectively.

Egg masses introduced to Auckland from Kobe hatched within the calendar year of oviposition (Fig. 2c) because they completed diapause on 2 November (average date for completion by 50% of oviposited population), and post-diapause was quickly completed in the November and December summer temperatures (Gray 2009) of the southern hemisphere. In contrast, egg masses introduced to Vancouver from Kobe did not hatch until well into the year following oviposition (Fig. 3c) because they completed diapause 25 December when winter temperatures were not optimal for subsequent post-diapause development (Gray 2009). Egg masses introduced by the Vladivostok–Vancouver route did not complete diapause until 17 March (due to the combination of late oviposition in Vladivostok and mild winters in Vancouver, which result in slow diapause development [Gray et al. 2001]) and hatched later than egg masses introduced from Kobe (Figs. 3c and 4c).

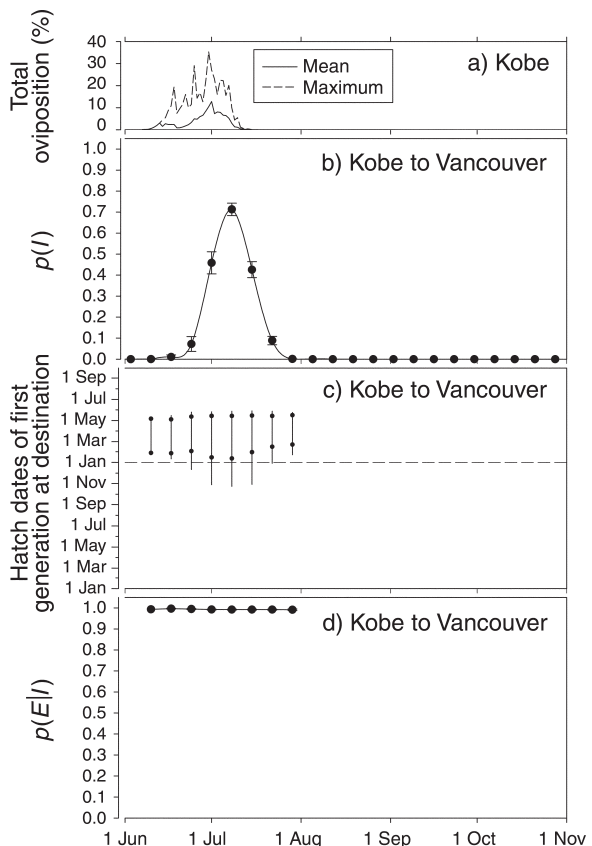


FIG. 3. (a) Daily gypsy moth oviposition frequency, as a percentage of season total, at Kobe, Japan, (b) probability of introduction [ $p(I)$ ; mean  $\pm$  SE], (c) first egg hatch period, and (d) probability of establishment given an introduction [ $p(E|I)$ ; mean  $\pm$  SE] in Vancouver, Canada, under a best-case scenario. Minimum daily oviposition frequency in Kobe was most often zero and is not shown. In panel (c) mean days of first and last egg hatch in Vancouver are shown by solid circles, and extremes are indicated by end points of vertical bars.

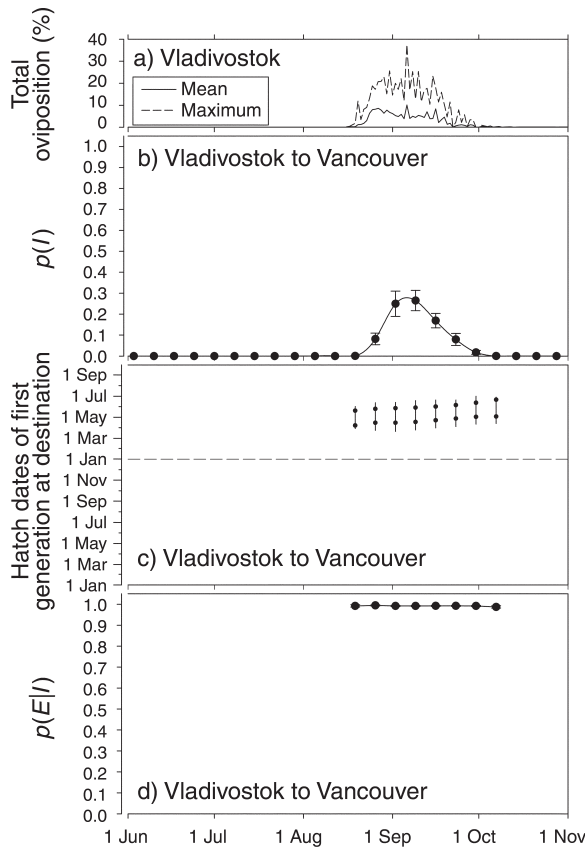


FIG. 4. (a) Daily gypsy moth oviposition frequency, as a percentage of season total, at Vladivostok, Russia, (b) probability of introduction [ $p(I)$ ; mean  $\pm$  SE], (c) first egg hatch period, and (d) probability of establishment given an introduction [ $p(E|I)$ ; mean  $\pm$  SE] in Vancouver, Canada, for each departure date under a best-case scenario. Minimum daily oviposition frequency in Vladivostok was most often zero and is not shown. In panel (c) mean days of first and last egg hatch in Vancouver are shown by solid circles, and extremes are indicated by end points of vertical bars.

The  $p(E|I)$  was higher in Vancouver ( $0.993 \pm 0.001$ ) than Auckland ( $0.439 \pm 0.021$ ) following transit from Kobe, and virtually equal in Vancouver following transit from Kobe and Vladivostok ( $0.992 \pm 0.001$ ) (Figs. 2d, 3d, and 4d). The  $p(E|I)$  in Vancouver was mostly unaffected by departure date from Kobe (Fig. 3d) and Vladivostok (Fig. 4d). In contrast, the  $p(E|I)$  in Auckland was 43% higher from a 29 July departure than from an 8 July departure from Kobe (Fig. 2d).

DISCUSSION

Phenological modeling in entomology has a history that dates at least to the French scientist de Réaumur (1683–1757), who published his observations on the effects of temperature on developmental rate (Egerton 2006). In the past century the most common use of insect phenology models has been perhaps in the area of pest management, where accurate timing of field activities is of obvious importance. Despite the equally obvious

importance of climate in defining species ranges (Ayres and Lombardero 2000, Kerdelhué et al. 2009, Robertson et al. 2009) phenology models have not been used commonly for this purpose. This may be due to the paucity of geographically robust phenology models that encompass an entire life cycle (as opposed to just the feeding stage[s], for example); thus, few are able to estimate climatic suitability for intergenerational survival. Insect establishment defines a species range, and it can occur only where intergenerational survival is consistently above a minimum threshold. Intergenerational survival is affected by host availability, mortality from natural enemies, and climatic suitability (i.e., the relative ability of the local climate to repeatedly satisfy temperature requirements for seasonal life cycle completion [Gray 2004, Robinet et al. 2007]). As shown here, the GLS model is geographically robust and multigenerational and is able to estimate one of the essential components of insect establishment.

Successful introduction of Asian gypsy moth requires two things. First, containers and/or ships must be present at the port of origin during egg oviposition. The  $p(I)$  increases as the temporal intersection between oviposition period and presence of containers and ships increases; ships depart with a greater abundance of egg masses. Second, the combined weather conditions of the origin, route, and destination must satisfy life cycle requirements; eggs must hatch at the destination. Phenological development and daily oviposition in Kobe are the same regardless of whether ships are destined for Auckland (Fig. 2a) or Vancouver (Fig. 3a); ship infestation levels are identical and weather conditions of the two routes were equally satisfactory [Kobe–Auckland  $p(I)$  = Kobe–Vancouver  $p(I)$ ], despite very large differences in the latitudinal changes that occurred during the routes (Kobe–Auckland, 71.5°; Kobe–Vancouver, 7.6°). Introduction to Vancouver from Vladivostok was less likely than from Kobe for two reasons: (1) a more prolonged oviposition period in

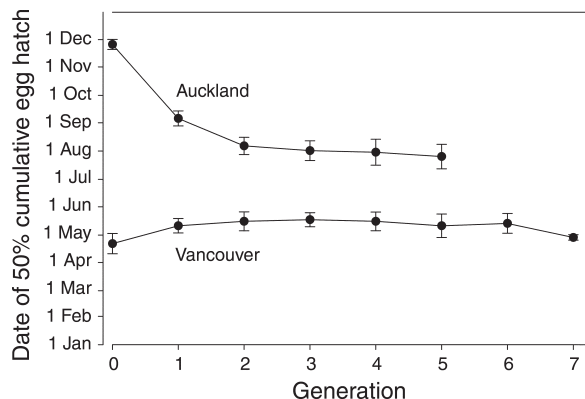


FIG. 5. Trend in date of 50% hatch at Auckland, New Zealand, and Vancouver, Canada, for seven generations following introduction from a 9 July departure from Kobe, Japan (mean  $\pm$  SE).

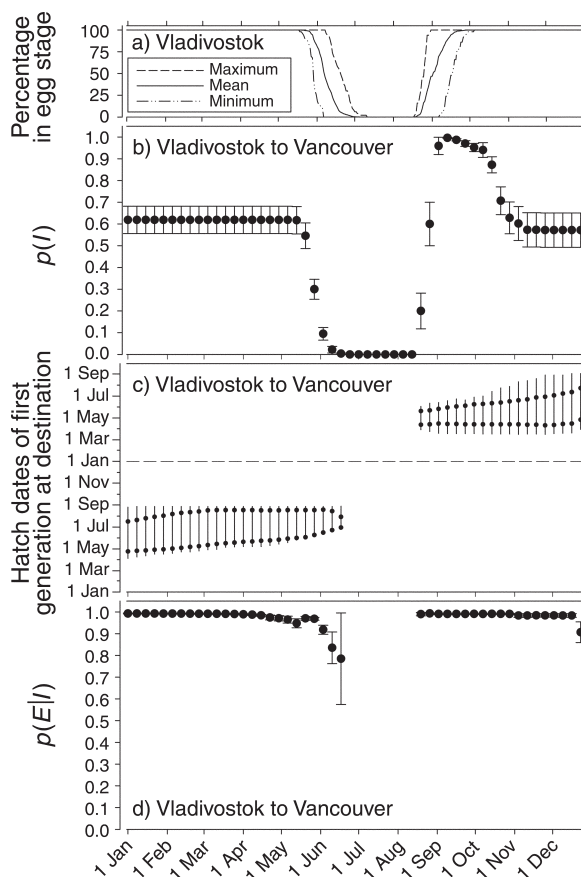


FIG. 6. (a) Gypsy moth egg abundance at Vladivostok, Russia, (b) probability of introduction [ $p(I)$ ; mean  $\pm$  SE], (c) first egg hatch period, and (d) probability of establishment given an introduction [ $p(E|I)$ ; mean  $\pm$  SE] in Vancouver, Canada, for each departure date under a worst-case scenario. Minimum daily oviposition frequency in Vladivostok was most often zero and is not shown. In panel (c) mean day of first and last egg hatch is shown by solid circles, and extremes are indicated by end points of vertical bars.

Vladivostok means fewer egg masses are laid per day, which results in a generally lower infestation on containers and ships that spend a short time in port; and (2) the later oviposition in Vladivostok results in higher mortality from the low temperatures that occur before the population has entered the cold-tolerant diapause phase (Gray 2004).

The probability of establishment given an introduction [ $p(E|I)$ ] depends on transit route, departure date, and the climate at the destination. The large latitudinal difference between Kobe and Auckland and the reversal of the seasons that occurs en route disrupted phenological development: a stable egg hatch pattern was not achieved for three generations following introduction (Fig. 5). Departure date affects  $p(E|I)$  (Fig. 2d) because a less optimal introduction date decreases intergenerational survival until stable seasonality is achieved. And

finally, the Auckland climate does not regularly produce high intergenerational survival even after stable phenological development has been achieved: high winter temperatures do not promote diapause development (Gray et al. 2001, Gray 2004), which results in a relatively low  $p(E|I)$  for all departure dates (Fig. 2d). Populations introduced to Vancouver very quickly achieved seasonal development (Fig. 5), and Vancouver's climate regularly produces high intergenerational survival rates, which results in a relatively uniform and high  $p(E|I)$ , regardless of departure date (Figs. 3d and 4d).

In the scenarios described heretofore, it was assumed that containers arrived at the port (origin) over a six-day period, ships arrived in the port only six days after the last container arrived, and ships spent only six days in port. These could be considered the "best-case scenarios" of well-run container and loading ports with tight schedules to which there is strict adherence. Unfortunately such scenarios may not always be the reality. In April 2009, ships representing  $\sim 10\%$  of the world's cargo capacity were idled in Asian ports and containers accumulated at ports due to the sudden economic downturn and falling demand for Asian goods (Klein and Cukier 2009). Under a "worst-case scenario," infested containers may remain in port and be loaded much later on departing ships, leading to high  $p(I)$  and  $p(E|I)$  for all departure dates except during the time when no eggs are present in the population at the origin (Fig. 6). As port efficiency declines (i.e., containers arrive over a longer period of time and the interval between container arrival and loading on a departing ship is extended),  $p(I)$  increases and the period with positive  $p(I)$  lengthens (Fig. 7). Potential reasons for the preponderance of gypsy moth interceptions in 1995–1998 is a change in container usage patterns (Ministry of Agriculture and Forestry Biosecurity New Zealand 2008).

The CFIA defines "high-risk vessels" (i.e., those with a potential to carry viable egg masses to Canada) as those that have visited Kobe between 1 June and 15 August or Vladivostok between 1 July and 30 September (Canadian Food Inspection Agency 2010). The USDA-APHIS uses 15 July–30 September for Vladivostok (USDA/APHIS/PPQ 2010). The CFIA defines "high-risk periods" (i.e., times when newly emerged first-instar larvae can disperse at the destination) as 1 March–15 October. The USDA-APHIS defines the period as 1 March–30 September for Oregon and Washington. These dates for high-risk vessels encompass the period of the best-case scenario when estimates of  $p(I) > 0$  in Kobe, but end one week too early in Vladivostok (Figs. 3a, b and 4a, b), and there is no distinction among the departure dates with varying  $p(I)$ . Under the worst-case scenario,  $p(I) > 0$  for a far longer period than that defined by the CFIA and USDA-APHIS for high-risk vessels. During a substantial portion of the high-risk periods defined by the CFIA and USDA-APHIS there are no newly emerged first-instar (i.e., dispersal-capable)

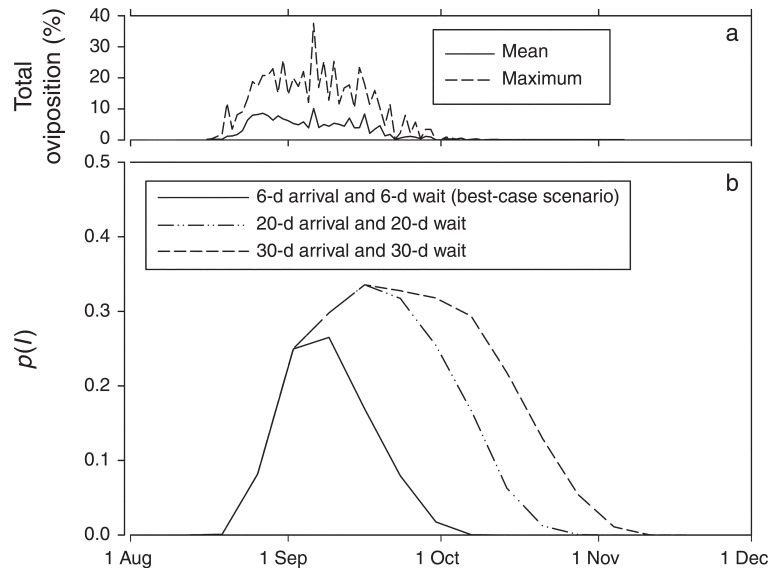


FIG. 7. (a) Daily gypsy moth oviposition frequency, as a percentage of season total, at Vladivostok, Russia, and (b) probability of introduction  $p(I)$  in Vancouver, Canada, for each departure date given different port efficiencies. Minimum daily oviposition frequency in Vladivostok was most often zero and is not shown. Port efficiencies differ in the number of days over which containers destined for a particular ship arrive at the port ( $x$ -d arrival) and the number of days a container waits at the port before being loaded on a departing ship ( $x$ -d wait).

larvae present. Thus, the CFIA and USDA-APHIS protocols simultaneously contain an unnecessary acceptance of risk (re: high-risk vessels) and a high aversion to risk (re: high-risk periods).

Although various authors have used the GLS model to estimate the risk of establishment, most examples have implemented GLS within the BioSIM framework of Régnière (1996) and have made certain assumptions for the simulations that are not specifically required by GLS and/or have not made full use of the GLS capabilities. For example, a single arbitrary date of oviposition was used to initiate GLS (Régnière and Nealis 2002, Logan et al. 2006, Pitt et al. 2007); oviposition in successive generations of multiyear simulations occurred on a single date using the date of peak (or possibly median) adult female emergence in the preceding generation (Logan et al. 2006, Pitt et al. 2007); a binomial (1 or 0) “establishment flag” was based on the simulated occurrence of an arbitrary phenological event before an arbitrary date (Logan et al. 2006, Pitt et al. 2007).

In many cases, an arbitrary oviposition date for initiation may be reasonable, and, in fact, Gray (2004) showed that egg hatch patterns are affected very little by oviposition date in GLS simulations under temperature conditions that prevail where gypsy moth is well established. However, using a single oviposition date to initiate GLS reduces the variability that occurs in a natural population and has a greater effect on hatch success and hatch pattern where climatic suitability (Gray 2004) is lower (Fig. 8). This variability is especially important in areas where the climate is

marginally suitable and true population persistence may be adversely affected by the increased variability in adult emergence and oviposition that would result from greater variability in egg hatch pattern (Robinet et al. 2007). Furthermore, where gypsy moth is not yet established there may be little evidence supporting an arbitrary date. For these reasons, the use of an arbitrary oviposition date should be avoided, and the built-in stabilization option of GLS (Gray 2004) should be used to determine a likely oviposition profile for each location in which it is run.

The use of the date of peak (or possibly median) adult female emergence in  $F_i$  to initiate all oviposition in  $F_{i+1}$  further reduces variability and in essence may “save” a portion of the population whose true simulated oviposition dates were later than the median and too late for survival of the oviposited eggs (Gray 2004). In the simulations described here, GLS maintained full phenological variability by using the emergence profile of adult females of  $F_i$  to simulate oviposition of  $F_{i+1}$ . Similarly, the use of a binomial (all or none) “establishment flag” ignores the potential risk posed by even a small fraction of the population surviving a generation. In the simulations described here GLS-2d calculated the mean intergenerational survival from the generations of each iteration and departure date combination. The probability of establishment given an introduction [ $p(E|I)$ ] for each departure date was estimated as the mean ( $\pm$ SE) of the 25 iterations. This metric is a better reflection than a binomial flag of the likelihood that seasonality will be maintained and establishment will be successful following transit and introduction.



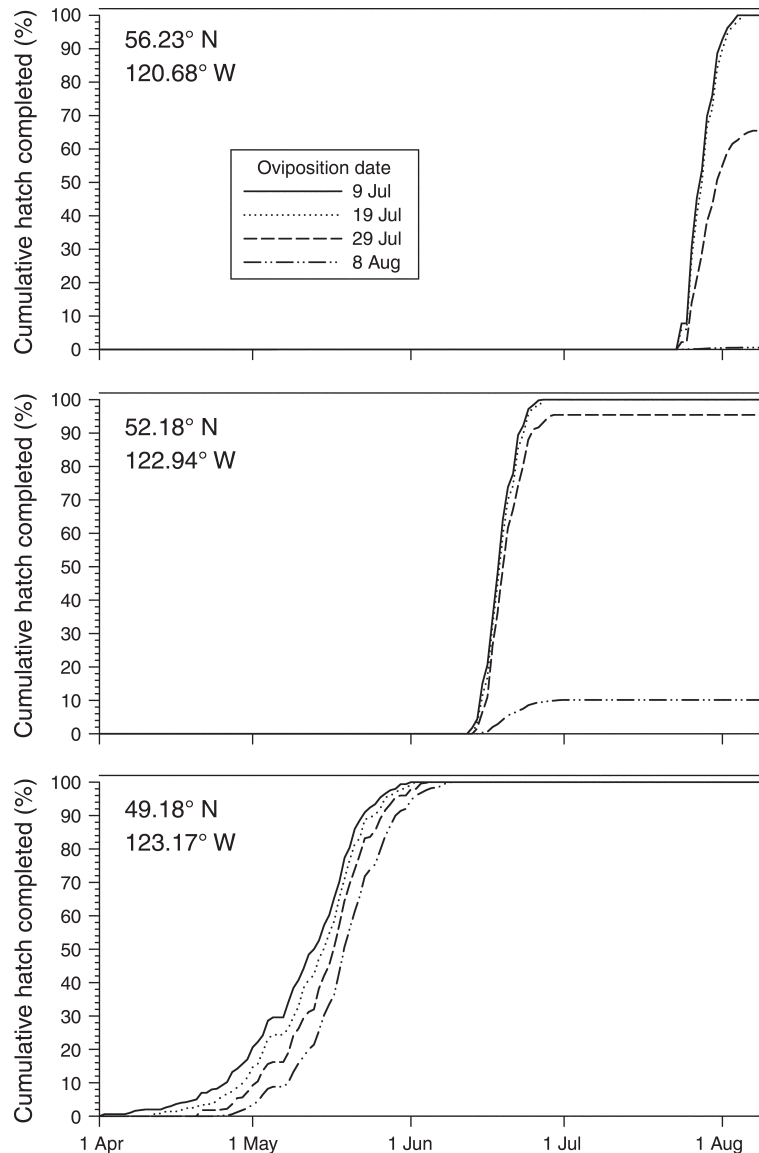


FIG. 8. Effect of arbitrary oviposition date on hatch pattern and hatch success at three locations of a south–north transect. Later oviposition dates have greater effect on hatch success at higher latitudes.

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#### LITERATURE CITED

- Allen, J. C., J. L. Foltz, W. N. Dixon, A. M. Liebhold, J. J. Colbert, J. Régnière, D. R. Gray, J. W. Wilder, and I. Christie. 1993. Will the gypsy moth become a pest in Florida? *Florida Entomologist* 76:102–113.
- Anonymous. 2008. Gypsy moth levy unchanged in 2008–09. *Biosecurity Magazine* 84:11.
- Ayres, M. P., and M. J. Lombardero. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Science of the Total Environment* 262:263–286.
- Biosecurity New Zealand. 2007. Joint decision-making and resourcing for readiness and incursion responses. Discussion paper. Biosecurity New Zealand, Wellington, New Zealand. (<http://www.biosecurity.govt.nz/strategy-and-consultation/consultation/discussion-documents/joint-decision-making>)
- Canadian Centre for Climate Modelling and Analysis. 2008. Canadian global circulation model. Version 3.1/T63 model output. ([http://www.cccma.ec.gc.ca/data/cgcm3/cgcm3\\_t63\\_20c3m.shtml](http://www.cccma.ec.gc.ca/data/cgcm3/cgcm3_t63_20c3m.shtml))
- Canadian Food Inspection Agency. 2010. Asian gypsy moth (*Lymantria dispar* L.): plant protection policy for marine vessels. Plant protection policy directive D-95-03. (<http://www.inspection.gc.ca/english/plaveg/protect/dir/d-95-03e.shtml>)
- Canadian Food Inspection Agency and U.S. Department of Agriculture. 2009. Asian gypsy moth alert. ([http://www.cbp.gov/linkhandler/cgov/border\\_security/port\\_activities/agro\\_inspection/agm\\_alerts.ctt/agm\\_alerts.doc](http://www.cbp.gov/linkhandler/cgov/border_security/port_activities/agro_inspection/agm_alerts.ctt/agm_alerts.doc))

- Earth Info. 2008. Global historical climatology network, global daily. (<http://www.earthinfo.com/databases/databases.htm>)
- Egerton, F. N. 2006. A history of the ecological sciences, part 21: Réaumur and his history of insects. *Bulletin of the Ecological Society of America* 87:212–224.
- Gray, D. R. 2004. The gypsy moth life stage model: landscape-wide estimates of gypsy moth establishment using a multi-generational phenology model. *Ecological Modelling* 176:155–171.
- Gray, D. R. 2009. Age-dependent postdiapause development in the gypsy moth (Lepidoptera: Lymantriidae) life stage model. *Environmental Entomology* 38:18–25.
- Gray, D. R., J. A. Logan, F. W. Ravlin, and J. A. Carlson. 1991. Toward a model of gypsy moth egg phenology: using respiration rates of individual eggs to determine temperature-time requirements of pre-diapause development. *Environmental Entomology* 20:1645–1652.
- Gray, D. R., F. W. Ravlin, and J. A. Braine. 2001. Diapause in the gypsy moth: a model of inhibition and development. *Journal of Insect Physiology* 47:173–184.
- Gray, D. R., F. W. Ravlin, J. Régnière, and J. A. Logan. 1995. Further advances toward a model of gypsy moth (*Lymantria dispar* (L.)) egg phenology: respiration rates and thermal responsiveness during diapause, and age-dependent developmental rates in postdiapause. *Journal of Insect Physiology* 41:247–256.
- Hopper, B. E. 1993. Pest risk analysis: defining the concept. International approaches to plant pest risk analysis. Pages 19–30 in *Proceedings of the APHIS/NAPPO International Workshop on the Identification, Assessment, and Management of Risks due to Exotic Agricultural Pests*, Ottawa, Canada. North American Plant Protection Organization, Ottawa, Ontario, Canada.
- Kerdelhué, C., L. Zane, M. Simonato, P. Salvato, J. Rousselet, A. Roques, and A. Battisti. 2009. Quaternary history and contemporary patterns in a currently expanding species. *BMC Evolutionary Biology* 9:1–14.
- Klein, B. P., and K. N. Cukier. 2009. Tamed tigers, distressed dragons; how export-led growth derailed Asia's economies. *Foreign Affairs* 88:8–16.
- Liebold, A. M., J. A. Halverson, and G. A. Elmes. 1992. Gypsy moth invasion in North America: a quantitative analysis. *Journal of Biogeography* 19:513–520.
- Liebold, A., V. Mastro, and P. Schaefer. 1989. Learning from the legacy of Leopold Trouvelot. *Bulletin of the Entomological Society of America* 35:20–22.
- Liebold, A. M., and P. C. Tobin. 2008. Population ecology of insect invasions and their management. *Annual Review of Entomology* 53:387–408.
- Lieth, H. 1974. *Phenology and seasonality modeling*. Springer-Verlag, New York, New York, USA.
- Logan, J. A., P. A. Casagrande, and A. M. Liebold. 1991. Modeling environment for simulation of gypsy moth (Lepidoptera: Lymantriidae) larval phenology. *Environmental Entomology* 20:1516–1525.
- Logan, J. A., J. Régnière, D. R. Gray, and A. S. Munson. 2006. Risk assessment in face of a changing environment: gypsy moth and climate change in Utah. *Ecological Applications* 17:101–117.
- Mason, C. J., and M. L. McManus. 1981. Larval dispersal of the gypsy moth. Pages 160–202 in C. C. Doane and M. L. McManus, editors. *The gypsy moth: research toward integrated pest management*. USDA Technical Bulletin 1584. USDA Forest Service, Washington, D.C., USA.
- Ministry of Agriculture and Forestry Biosecurity New Zealand. 2008. Pest risk analysis for six moth species: lessons for the biosecurity system on managing hitchhiker organisms. Ministry of Agriculture and Forestry, Biosecurity New Zealand Wellington, New Zealand. (<http://www.biosecurity.govt.nz/files/biosec/consult/risk-analysis-moths.pdf>)
- New Zealand National Institute of Water and Atmospheric Research. 2002. National climate database. (<http://cliflo.niwa.co.nz/>)
- Pitt, J. P. W., J. Régnière, and S. Worner. 2007. Risk assessment of the gypsy moth, *Lymantria dispar* (L.), in New Zealand based on phenology modelling. *International Journal of Biometeorology* 51:295–305.
- Régnière, J. 1996. Generalized approach to landscape-wide seasonal forecasting with temperature-driven simulation models. *Environmental Entomology* 25:869–881.
- Régnière, J., and V. Nealis. 2002. Modelling seasonality of gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), to evaluate probability of its persistence in novel environments. *Canadian Entomologist* 134:805–824.
- Robertson, C., M. A. Wulder, B. Boots, T. A. Nelson, and D. E. Jelinski. 2009. Spatial-temporal analysis of species range expansion: the case of the mountain pine beetle, *Dendroctonus ponderosae*. *Journal of Biogeography* 36:1446–1458.
- Robinet, C., A. E. Liebhold, and D. R. Gray. 2007. Variation in developmental time affects mating success and Allee effects. *Oikos* 116:1227–1237.
- Schmoldt, D. L. 2001. Application of artificial intelligence to risk analysis for forested ecosystems. Pages 49–74 in K. Von Gadow, editor. *Risk analysis in forest management*. Kluwer Academic, Dordrecht, The Netherlands.
- Sharov, A. A., and A. M. Liebhold. 1998. Model of slowing the spread of gypsy moth (Lepidoptera: Lymantriidae) with a barrier zone. *Ecological Applications* 8:1170–1179.
- Sheehan, K. A. 1992. User's guide for GMPHEN: gypsy moth phenology model. General Technical Report NE-158. USDA, Forest Service, Radnor, Pennsylvania, USA.
- Shigesada, N., and K. Kawasaki. 1997. *Biological invasions: theory and practice*. Oxford University Press, Oxford, UK.
- Sutherst, R. W., and G. F. Maywald. 1985. A computerized system for matching climates in ecology. *Agriculture, Ecosystems and Environment* 13:281–299.
- Sutherst, R. W., J. P. Spradbery, and G. F. Maywald. 1989. The potential geographical distribution of the Old World screw-worm, *Chrysomya bezziana*. *Medical and Veterinary Entomology* 3:273–280.
- Tatem, A. J., S. I. Hay, and D. J. Rogers. 2006. Global traffic and disease vector dispersal. *Proceedings of the National Academy of Sciences USA* 103:6242–6247.
- USDA/APHIS/PPQ [U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Plant Protection and Quarantine]. 2010. Manual for agricultural clearance. ([http://www.aphis.usda.gov/import\\_export/plants/manuals/ports/downloads/mac.pdf](http://www.aphis.usda.gov/import_export/plants/manuals/ports/downloads/mac.pdf))
- Walter, H., H. Harnickell, and D. Mueller-Dombois. 1975. *Climate-diagram maps of the individual continents and the ecological climatic regions of the earth*. Springer, New York, New York, USA.
- Weseloh, R. M. 1997. Evidence for limited dispersal of larval gypsy moth, *Lymantria dispar* L. (Lepidoptera: Lymantriidae). *Canadian Entomologist* 129:355–361.
- Worner, S. P. 1988. Ecoclimatic assessment of potential establishment of exotic pests. *Journal of Economic Entomology* 81:973–983.