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Research

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Heat treatments to kill eggs of two invasive forest insects: *Lycorma delicatula* (Hemiptera: Fulgoridae) and *Lymantria dispar* (Lepidoptera: Erebidae)

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The spotted lanternfly (*Lycorma delicatula*) and spongy moth (*Lymantria dispar*) are notorious invasive forest pests that are spread through human-mediated transport to invade new habitats. In this study, spotted lanternfly and spongy moth eggs were exposed to various temperature-exposure time (35 to 70 °C and 15 to 135 min) treatments in the laboratory. Spotted lanternfly egg masses were collected from various sites in 2022 and 2023, while the spongy moth egg masses were obtained from lab-reared colonies. Heat treatments were applied using an Isotemp microbiological incubator in the spring of 2023 and the spring and fall of 2024. No eggs of either species hatched when exposed to temperatures ≥ 60 °C for durations longer than 15 min. Spotted lanternfly egg hatch declined at temperatures ≥ 45 °C, while reduced hatch of spongy moth eggs was not observed until temperatures reached ≥ 50 °C. The season (spring or fall) in which the eggs were heat treated did not affect the hatch rate of spotted lanternfly eggs; however, spongy moth eggs were more vulnerable in the fall than in the spring. These findings suggest that heat treatment regimes that are already being used to kill insects in wood may effectively kill the eggs of both species on various substrates and that protocols for killing eggs at lower temperatures on more sensitive substrates may be possible by using longer-duration exposures.

Keywords: egg hatch, spotted lanternfly, spongy moth, heat treatment

Introduction

Invasive species are often capable of rapid dispersal both in time and space either naturally or by human-aided means, rapid growth rates characterized by short generation intervals, and a remarkable range of tolerance for various environmental conditions. These traits significantly enhance their ability to establish and thrive in new environments and allow them to effectively respond to shifts in climate patterns (Poland et al. 2021). However, the introduction of invasive species can have devastating consequences on forest ecosystems (Pimentel et al. 2005) by outcompeting native species for resources, disrupting established food webs, and altering habitat structure, leading to a decline in biodiversity (Wilcove et al. 1998). Invasive insects in particular can also cause significant damage to tree health, increase tree mortality rates, and create conditions that are more favorable for further invasions (Aukema et al. 2011). Ultimately, the economic costs associated with managing invasive species and restoring affected forests can be substantial, underscoring the critical need for effective monitoring and management strategies (Pimentel et al. 2001).

Two invasive forest pests of high ecological and economic importance that are known to disperse by human-aided means are the spotted lanternfly, *Lycorma delicatula* (White) (Hemiptera: Fulgoridae), and the spongy moth, *Lymantria dispar* L. (Lepidoptera: Erebidae). Both species are highly polyphagous, feeding on more than 100 species of plants in the northeastern United States and continuing to expand their range and cause damage despite efforts to slow their spread and control them (Cook et al. 2021, Mastro et al. 2021, Jones et al. 2022). The spotted lanternfly is a univoltine sap-feeding planthopper native to Asia that was introduced into the United States in 2014 (Barringer et al. 2015). Although tree of heaven, *Ailanthus altissima*, is recognized as a primary host for this species, the spotted lanternfly feeds on around 100 hosts and damages several agricultural, landscape, and forest host plants with an increasing potential for economic and ecological impacts (Urban and Leach 2023). The spongy moth is a univoltine, foliage-feeding moth native to the Palearctic region that was also introduced into eastern North America (Rindos and Liebhold 2023) and can utilize more than 300 species of host plants, including deciduous and coniferous trees (Rindos and Liebhold 2023). Unlike the spongy moth (*L. dispar dispar*) that is already established in North America, the flighted spongy moth complex (*L. dispar asiatica* and *L. dispar japonica*) poses a significant threat to North America if populations were to establish, as females of these subspecies are capable of flight, enabling them to spread more quickly (Srivastava et al. 2021). Both spotted lanternfly and spongy moth lay their eggs on tree trunks, rocks, or other available substrates. The spongy moth overwinters as mature embryonic larvae inside the eggs (Keena 2016), while the spotted lanternfly overwinters as an egg in the early stages of development (Shim and Lee 2015).

Like other ectotherms, insects are highly vulnerable to changes in abiotic factors in the surrounding environment, and environmental conditions strongly impact their biology (Colinet et al. 2015, Harvey et al. 2020). Temperature is one of insects' most challenging abiotic stressors, and it can determine their survival, population dynamics, and distribution (Zhou et al. 2015). Extreme temperatures that approach or surpass critical thermal thresholds increase mortality rates (Richter et al. 2010, Sinclair et al. 2012) due to injuries that require physiological or biochemical repairs (Feder and Hoffman 1999, Colinet et al. 2015). Extreme heat exposure imposes substantial thermal stress on insects by disturbing the balance of macromolecules like DNA, proteins, and membrane lipids, resulting in structural and functional deterioration (Perez and Aron 2020). Intense thermal exposure also has the potential to result in the demise of cells, necrosis of tissues, and, ultimately, the death of the affected individual (Perez and Aron 2020).

Insects experience deleterious effects at temperatures above 42 °C (Neven and Mitcham 1996), and temperatures above 62 °C kill stored-product insect pests in less than one minute (Fields and White 2002). Temperatures ≥ 50 °C have been used as a post-harvest treatment to kill insects in stored products and fruits (Velazquez et al. 2010, Hansen et al. 2011). Heat treatment is one of the approved treatments (International Standards Phytosanitary Measures [ISPM] 15) for solid wood packaging materials to kill wood-boring insects that they may contain, which involves heating wood until the inner core temperature reaches 56 °C and remains constant for a minimum of 30 min (Haack et al. 2014, FAO 2019). No specific standards for heat treatments exist for insects that are spread through human-mediated transport, so there is a critical need to find environmentally friendly ways to kill these invasive insects to help stop their human-aided dispersal.

The primary variables of thermal treatment are temperature and exposure time (Sharp 1993, Hallman and Armstrong 1994). Other crucial elements impacting insect survival within heat treatment experiments include the treatment substrate, humidity, oxygen concentration, evenness of heating, rate of heating, and final temperature (Wang et al. 2009). This study focuses on understanding the upper thermal tolerance of these species' eggs by exposing them to different high temperatures for various durations and then assessing the percentage of hatch. These results may help identify potential specific heat treatments that could be used to develop a novel regulatory treatment to aid in preventing the spread of these insects through human-aided means.

Materials and Methods

Spotted Lanternfly Egg Mass Sources

Spotted lanternfly egg masses were collected from various sites representing distinct cold hardiness zones. This was done to account for any variation that may occur in heat tolerance since previous work has shown populations vary in thermal responses (Keena et al. 2023). Egg mass collection began in early October 2022 and 2023 and concluded in early December 2022 and late November 2023. Information about collection sites and the number of egg masses used in the experiments are summarized in Table 1. The host bark was carefully cut ≥0.5 cm from the margin of each egg mass, then the egg mass was excised intact with the bark section (Keena and Nielsen 2021). Egg masses were then transported to the USDA Forest Service Quarantine Laboratory in Ansonia, Connecticut, adhering to conditions in valid state and federal permits. To prevent fungal growth and minimize moisture content, the eggs' bark sections were air-dried in the laboratory on a raised screen under a laminar flow hood at room temperature for 30 to 60 min (Keena and Nielsen 2021). Egg masses were then held in 55 × 15 mm vented petri dishes. Egg masses averaged 32 ± 1 eggs per mass in 2023 and 32 ± 0.4 eggs per mass in 2024.

Spongy Moth Egg Mass Sources

Egg masses from two distinct laboratory colonies of spongy moth were used. The *L. dispar asiatica* population, abbreviated "RM," originated in the Russian Far East (Mineralni, Primorski Province, Russia, 44.10°N and 133.15°E) and was collected in August 1992. The *L. dispar dispar* population, abbreviated "CT," originated in the United States (Bethany, New Haven County, Connecticut, 41.25° N and 73.00° W) and was collected in March 1994. Both populations were carefully maintained under quarantine conditions at the USDA Forest Service Quarantine Laboratory in Ansonia, Connecticut. The RM and CT egg masses corresponded to the 41st and 44th laboratory generations in the first year of study and 42nd and 45th in the second year, respectively. To start each laboratory generation, the eggs from one hundred egg masses from the previous generation were mixed to ensure genetic diversity. Moths were reared from randomly selected eggs in walk-in environmental chambers, kept at a temperature of 25 °C, relative humidity of 60%, and subjected to a 16:8 (L:D) hour photoperiod for egg mass production. Larvae were reared in cohorts of 8 individuals, each placed in 236 ml transparent plastic cups topped with paper lids (Sweetheart, Chicago, IL) (Keena 2022). During development, larvae were given a diet high in wheat germ with the appropriate amount of iron for each population (Bell et al. 1981, Keena 2022). Newly formed pupae were harvested and held separately by sex in 1.6 L paper containers (Solo 3T1, Solo Cup Operating Corp., Dallas, TX, USA). Pupae were checked daily and adult eclosion was recorded. The males were held in groups of up to 5 at 15 °C to prolong viability while individual females were placed in 236 ml paper cups labeled with population and eclosion date. Females' cups were used for mating by introducing individual males of the same population randomly chosen from those no more than 6 d old. The cups were covered with 6 × 6-inch plastic bags secured with rubber bands. Eggs were held at 25 °C for a minimum of 25 d to ensure embryonation. Then, eggs were removed by cutting

Table 1. Spotted lanternfly egg mass collection in 2022 and 2023.

Collection site closest city, state	Geographical coordinates	Plant cold hardiness zone	Number of egg masses	Collection date
2022				
Staten Island, New York	40.54°N, 74.12° W	7B	56	Oct.14
High Bridge, New Jersey	40.66°N, 74.92° W	6A-6B	36	Oct. 26
Lakehurst, New Jersey	40.02°N, 74.30° W	7A	68	Nov. 01
Lakehurst, New Jersey	40.02°N,74.33° W	7A	11	Nov. 01
Cookstown, New Jersey	40.04°N, 74.57° W	7A	74	Nov. 02
Kernersville, North Carolina	36.09° N, 80.06 W	7B	41	Oct. 04
Pittsburgh, Pennsylvania	40.42°N, 80.00° W	6B	31	Oct. 24
Springfield, Massachusetts	42.15° N, 72.52°W	6A-6B	32	Dec. 02
Fairfield, Connecticut	41.13°N,73.29° W	7A	24	Oct. 06 to Nov. 23
2023				
Greensburg, Pennsylvania	40.31°N, 79.59°W	6A	12	Oct. 16
Greensburg, Pennsylvania	40.31°N, 79.54°W	6A	46	Oct. 16
Pittsburgh, Pennsylvania	40.43°N, 79.90°W	6B	32	Oct. 17
Moonachie, New Jersey	40.84°N, 74.05°W	7A	113	Oct. 18
Fairfield, Connecticut	41.13°N, 73.29°W	7A	71	Oct. 18
Milford, Connecticut	41.24°N, 73.03°W	7A	160	Oct. 26
Milford, Connecticut	41.24°N, 73.03°W	7A	107	Nov. 28
Kernersville, North Carolina	36.10°N, 80.06°W	7B	55	Nov. 8
Ridgefield Park, New Jersey	40.86°N, 74.08°W	7A	64	Nov. 15
Middletown, New Jersey	40.39°N, 74.16°W	7A	31	Nov. 15
Huntington area, Pennsylvania	Multiple sites in PA	6B or 7A	242	Late Nov

around each egg mass deposited on the cup's wall, maintaining a 5-mm border (Keena 2022). Spongy moth egg masses typically contain large numbers of eggs (2023 CT 963 ± 12 eggs, 2024 CT 933 ± 18 eggs, 2023 RM 842 ± 11 eggs, 2024 RM 770 ± 17 eggs), so each egg mass was halved longitudinally using a spatula and the paper was cut with scissors. Spongy moth eggs are suspended in a matrix of hairs throughout so there should have been minimal differences between the eggs in exposure. Half egg masses were held in separate 100 × 15 mm petri dishes. Adult individuals from each population reared from these egg masses were documented as voucher specimens and deposited at the Entomology Division of the Yale Peabody Museum of Natural History in New Haven, CT.

Heat Treatments 2023

Spongy moth egg masses were initially held at 5 °C for 28 to 31 d to acclimate them before placing them in the alternating temperature regime, while spotted lanternfly egg masses were placed directly in the regime after processing. The alternating regime was designed to replicate climate normal (1981-2010 NOAA) weather conditions in Scranton, Pennsylvania using the weekly average maximum and minimum climate normal temperatures, relative humidity, and light cycle. A Percival I66VL chamber was set to ramp between the weekly maximum and minimum temperatures, and all set points were changed weekly.

In March, egg masses of both species were removed from the alternating regime and treated. Spotted lanternfly and spongy moth egg masses were affixed to wooden boards (30 × 30 cm by 3 mm thick balsa wood) using pins, with each board holding up to 36 egg masses. They were then subjected to heat treatments in a laboratory incubator (Fisherbrand Isotemp Microbiological Incubator 180L, Thermo Fisher Scientific, Waltham, MA). Treatments were applied to half of the egg masses randomly assigned to each treatment at one time, with about a week separating the cohorts.

Sixteen different time-temperature treatments were applied to spotted lanternfly egg masses (19 to 24 per treatment, 358 total). A total of 21 egg masses representing all sites were held as controls. Egg masses were assigned so that the number of egg masses from each site in each treatment was kept the same. Twenty-six time-temperature treatments were applied to spongy moth egg masses (24 to 26 per population per treatment, 913 total). Both insects' egg masses were exposed to various combinations of temperatures and durations ranging from 35 to 70 °C and 15 to 120 min; treatments are detailed in Table 2. Each time the incubator door was opened, the temperature dropped below the set point. The temperature it dropped to was recorded and the warmup phase was monitored by recording the time it took to warm each degree back to the set point. The timer for the treatment duration was started when the temperature was one degree below the set point, ensuring that the eggs received the designated heat for the specified time.

Following treatment, each spongy moth egg mass was transferred to a clean 100 × 15 mm plastic petri dish (no loose untreated eggs). Petri dishes were held by treatment in opaque plastic bins (46 × 28 × 16.5 cm) on a piece of plastic gridding cut the same size as the bottom of the container. A small amount of water was added, and thick pieces of clear plastic were taped to the top of the bins to maintain humidity. Spotted lanternfly egg masses were moved to clean petri dishes (35 × 10 mm) and kept in clear plastic cups placed in clear plastic boxes (43 × 30 × 18 cm). All egg masses were then transferred to a chamber at 25 °C, 60% RH, and 16:8 (L:D) photoperiod until the hatch was complete. Control treatments were removed from the alternating regime and placed directly into 25 °C. Egg masses were monitored daily, and hatch was removed and recorded until no hatch occurred for 30 d. Then, the covering of the eggs was removed to count the number of unhatched eggs and determine embryonation. The powdery gray covering of the spotted lanternfly eggs was removed using a fine brush, and then all eggs were counted. The tan hair covering of the spongy moth eggs was removed by scraping the egg mass off the paper into a container with a fine wire mesh bottom and using a vacuum below the screen while carefully brushing the eggs using a stiff brush. The clean eggs were then applied to a piece of clear tape and placed on paper for counting. The number of unhatched eggs was recorded, and the percentage hatch was calculated. Unembryonated spongy moth eggs were also counted; these were then subtracted from the

Table 2. Temperature and time duration used in heat treatment study on spotted lanternfly and spongy moth in 2023 (top) and 2024 (bottom). The black cells in the table indicate treatments applied to both insects, the diamonds represent treatments applied only to spongy moth, and circles indicate treatments specific to spotted lanternfly.

		Duration (mins)								
Year	Temperature (°C)	15	30	45	60	75	90	105	120	135
2023	35	■	■		◆				◆	
2023	40	■	■		◆				◆	
2023	45	■	■		■				■	
2023	50	■	■		◆				◆	
2023	55	■	■		◆					
2023	60	■	■		◆					
2023	65	■	◆							
2023	70	■	◆							
2024	45				○	○	○	○	○	○
2024	50	■	■	■	■	◆				
2024	55	○	○	○						
2024	60	○	○							

total number of unhatched eggs so the percentage hatch of only the embryonated eggs could be calculated. Embryonation was determined by examining the eggs under a microscope; unembryonated eggs were distinguished by their pale color in contrast to the dark brown embryonated ones.

Heat Treatments 2024

In the second year of the study, treatments were selected based on the results obtained in 2023 and were applied to both species' egg masses in the fall (just after eggs had embryonated) and spring (March, as in 2023). Treatments were applied in the same way and using the same equipment as in 2023. After treatment, egg masses were returned to the alternating regime instead of being moved to 25 °C.

Spotted lanternfly egg masses collected in October were held in a growth chamber at 20 °C, 65% RH, and 16:8 L:D for at least 2 wk after arriving in the laboratory to ensure embryo development but no diapause induction, which occurs with exposure to chill (Keena and Nielsen 2021). Some of these egg masses were used in both the fall and spring treatments. Egg masses collected from CT in November were put directly into the alternating regime; those from PA and NC were given a week at 10 °C, followed by a week at 5 °C for the PA egg masses, to acclimate them before placing them in the alternating regime, which was already set at winter temperatures. These egg masses were used only for the spring treatments, as they could have been in different stages of diapause when brought into the laboratory, while the fall treatment egg masses were all freshly embryonated and not in diapause yet. Egg masses were assigned to keep the number from each population the same across the treatments within these collection groups.

Nine hundred and thirty-two spotted lanternfly egg masses were used: 20 egg masses per treatment in the fall and 34 egg masses per treatment in the spring. There was a total of 52 control egg masses, representing all of the collection sites. Egg masses were exposed to heat treatments that varied in temperature (45 to 60 °C) and duration (15 to 135 min, Table 2). As in the 2023 study, egg masses were treated in two waves (half of the egg masses each) about a week apart. Temperatures were monitored during the incubator warm-up and the duration timer was started at one degree below the set point as in 2023.

The experiments also used 156 spongy moth egg masses per population, with 26 half egg masses per treatment in both fall and spring. One half of each egg mass was used for the fall treatments, and the second half was used for the spring treatments. Those intended for spring treatments were put directly into the alternating temperature regime, while those for the fall treatments were treated before being placed in the alternating regime after embryonation at 25 °C. Egg masses were exposed to 50 °C for durations ranging from 15 to 75 min in both the fall and spring treatments (Table 2). Fall heat treatments were applied in the first week of October 2023, and spring treatments were applied in mid-March 2024. Egg masses were transferred to the alternating regime immediately after treatment and held there until hatch was complete. Control egg masses were held at room temperature for the same length of time it took to heat treat egg masses and were then transferred to the alternating regime. Egg hatch was monitored daily and newly emerged larvae and nymphs were counted and removed daily. At the end of the study, the thickness of the bark on which the spotted lanternfly egg masses were treated was also measured to assess its potential effect on the heat treatments and subsequent egg hatch. A similar process was followed in the second year to determine the percent hatch for both insects.

Statistical Analysis

SAS version 9.4 (SAS Institute 2015) was used for statistical data analysis. Shapiro-Wilk and Anderson-Darling tests were used to evaluate the normality of data. Long right tails were found for some of the data, so a gamma distribution, which handles this type of data distribution, was used. PROC GLIMMIX, a generalized linear mixed model, was used to evaluate the fixed effects of treatment and season (2024 study only) on the percentage of egg hatch. Spotted lanternfly average number of days to hatch in the 2023 study was also evaluated using GLIMMIX and treatment as a fixed effect. In both 2023 and 2024, strain was used as a random effect in the models for both insects. A beta distribution with a logit link function was used for the percentage data, while a gamma distribution with a log link function was used for all the other data. As the values of zero and one cannot be fitted in a beta distribution, they were replaced with 0.0001 and 0.9999, respectively. Significant differences between means were evaluated using the Tukey–Kramer post-hoc analysis and $\alpha = 0.05$. Residuals for each model were assessed for normality, and the homogeneity of variance in each temperature treatment was checked using Levene's test to ensure the variances were equal between treatments. Linear regression was used to assess the relationship between the duration of heat exposure and the percentage hatch of egg masses at each temperature, which allowed an estimation of the rate of decrease in survival with increasing durations of exposure to specific temperatures.

Results

Temperature Treatments

When the incubator door was opened to place the egg masses inside, the temperature dropped to 2 to 6.3 °C below the set point in 2023 and 1.4 to 2.6 °C below in 2024 (Table 3). The time needed to warm up from two degrees below the set point to one degree below ranged from 2 to 12.8 min in 2023 and 1.4 to 4 min in 2024. With practice, methods were found to have the incubator door open for a shorter period in 2024 than in 2023.

2023 Study

The effect of different temperature-exposure time treatments on the spotted lanternfly egg hatch parameters in the first year of the study is shown in Table 4. The percentage of egg masses with hatch was 71% in the control and ranged from 0 to 75 in other treatments. The egg masses in the control treatment had a low mean percentage hatch (19.4) that did not differ significantly from the other treatments, but treatment still had a significant effect on percentage hatch ($F = 3.06$; df = 16, 332.6; $P < 0.0001$). The mean percentage hatch of an egg mass decreased, as did the number of egg masses that had hatch, with increasing temperatures above 45 °C. The shortest and longest mean time to hatch was 24.08 d at 40 °C for 30 min and 33.94 d at 50 °C for 30 min, respectively, and treatment did not have a significant effect on average time to hatch ($F = 1.62$; df = 12, 108.2; $P = 0.0957$).

A significant difference in the spongy moth egg hatch rates was observed among the treatments in 2023 ($F = 12.2$; df = 26, 772; $P < 0.0001$). Egg hatch decreased sharply at 50 °C (Fig. 1). At all temperatures and durations below 50 °C, percentage hatch was greater than 90%, not significantly different from the control. However, hatch rates dropped to around 60% when eggs were exposed to 50 °C for 15 min and less than 30% at 50 °C for 30 min, although there was substantial variation in percentage hatch between individual egg masses. Only 6 larvae hatched from a single half-egg mass when exposed to 50 °C for 60 min. There was no hatch at higher temperatures or durations at 50 °C except for a total of 60 eggs hatched from 3 egg masses when exposed to 55 °C for 15 min.

2024 Study

The season in which the heat treatments were applied had no significant effect on spotted lanternfly egg mass hatch ($F = 1.02$; df = 2, 437.2; $P = 0.36$), so these data were consolidated from the two seasons for analysis. Treatment had a significant effect on spotted lanternfly hatch in 2024 ($F = 24.45$; df = 10, 544.5; $P < 0.0001$). Percentage hatch in the control was 71%, significantly higher than all temperature-time combinations. At 45 °C, percentage hatch decreased at a rate of 0.96 per minute of exposure and then stayed at ≤ 0.6 percentage hatch from 75 to 120 min of exposure (Fig. 2A). Only 4 eggs hatched after 90 min and 3 after 120 min of exposure to 45 °C. The relationships between the duration of heat exposure and the percentage hatch of egg masses at each temperature are shown in Fig. 2. At 50 °C, percentage hatch decreased at a rate of 2.37 percentage hatch per minute of exposure and then stayed at ≤ 0.15 percentage hatch from 30 to 45 min of exposure (Fig. 2B). At 55 °C, percentage hatch declined more rapidly, decreasing at 4.74 percentage hatch per minute, with only 0.1 percentage hatch after 15 min and no hatch at longer durations (Fig. 2C).

Neither spongy moth strain ($F = 0.93$; df = 1, 442.5; $P = 0.34$) nor the interaction between strain and treatment ($F = 1.59$; df = 4, 442.5; $P = 0.17$) had a significant effect on percentage hatch, so the strains were combined for further analysis. The season in which treatments were applied (fall or spring) ($F = 12.3$; df = 1, 453; $P = 0.0005$) and the interaction between treatment and season ($F = 8.57$; df = 3, 453; $P < 0.0001$) both had a significant effect on percentage hatch, so the seasons are presented separately (Fig. 3). The relationships between the duration of heat exposure and the percentage hatch of egg masses at each temperature are shown in Fig. 3. In the fall, percentage hatch decreased at a rate of 2.94 percentage hatch per minute of exposure (Fig. 3A), while in the spring it decreased at a rate of 3.15 percentage hatch per minute of exposure (Fig. 3B). In addition, a few eggs hatched after 60 min of exposure to 50 °C in the fall, but there was no hatch at that duration in the spring.

Discussion

This study evaluated duration-dependent effects of environmental heating as a control mechanism for two unique invasive forest and agricultural pest insects. Findings identified different levels of vulnerability between species, as well as a seasonal influence which could potentially be exploited in control strategies for each species.

Table 3. Profile of heat treatments showing the rate of temperature increase as temperatures approached the set points.

Set point temperature	Initial temperature	Time (min) to warm from two to one degree below set temperature	Time (min) from the start (one degree below) to set temperature
2023			
35 °C	33.0 ± 0.34 °C	2.0 ± 0.00	5
40 °C	37.8 ± 0.31 °C	2.0 ± 0.71	5.7 ± 2.0
45 °C	41.5 ± 0.50 °C	6.2 ± 0.98	3.3 ± 2.9
50 °C	46.3 ± 0.29 °C	12.6 ± 2.00	22.5 ± 11.5
55 °C	50.6 ± 0.70 °C	5.3 ± 0.23	4.5 ± 3.5
60 °C	55.7 ± 0.67 °C	6.4 ± 1.83	4.7 ± 2.7
65 °C	58.4 ± 0.95 °C	9.0 ± 4.00	8
70 °C	63.6 ± 1.01 °C	12.8 ± 3.33	12
2024			
45 °C	43.4 ± 0.10 °C	1.4 ± 0.24	8.6 ± 0.4
50 °C	47.7 ± 0.13 °C	4.0 ± 1.04	7.8 ± 0.41
55 °C	52.8 ± 0.04 °C	2.0 ± 0.23	7.2 ± 0.40
60 °C	57.4 ± 0.13 °C	2.3 ± 0.25	7.4 ± 0.50

Table 4. Mean (± SE) for various spotted lanternfly egg hatch parameters under different 2023 temperature-time treatments.

Temperature-time regime	Number of egg masses	Percentage of egg masses with hatch	Mean time to hatch (days)	Mean percentage hatch for an egg mass
Control	21	71	29.17 ± 1.79 ab	19.4 ± 6.1 ab
35 °C for 15 min.	21	62	26.18 ± 1.69 ab	25.1 ± 7.0 a
35 °C for 30 min.	24	75	27.60 ± 1.64 ab	24.0 ± 6.7 ab
40 °C for 15 min.	21	48	29.04 ± 1.98 ab	14.7 ± 5.1 ab
40 °C for 30 min.	22	64	24.08 ± 1.53 a	28.0 ± 7.4 a
45 °C for 15 min.	22	73	26.73 ± 1.63 ab	4.7 ± 2.5 a
45 °C for 30 min.	20	55	31.35 ± 2.15 b	1.5 ± 5.1ab
45 °C for 60 min.	21	57	25.81 ± 1.73 ab	18.1 ± 5.8 ab
45 °C for 120 min.	19	32	26.56 ± 2.30 ab	27.1 ± 7.3b
50 °C for 15 min.	21	33	26.39 ± 2.13 ab	5.0 ± 2.5b
50 °C for 30 min.	21	5	33.94 ± 6.62 ab	0.1 ± 0.3 ab
55 °C for 15 min.	21	0	26.13 ± 5.00 ab	0.1 ± 0.3 ab
60 °C for 15 min.	21	0	29.33 ± 6.18 ab	0.3 ± 0.5 ab

Means followed by a different letter within a column are significantly different from each other at $P < 0.05$ using Tukey-Kramer post hoc test (SAS Institute 2015).

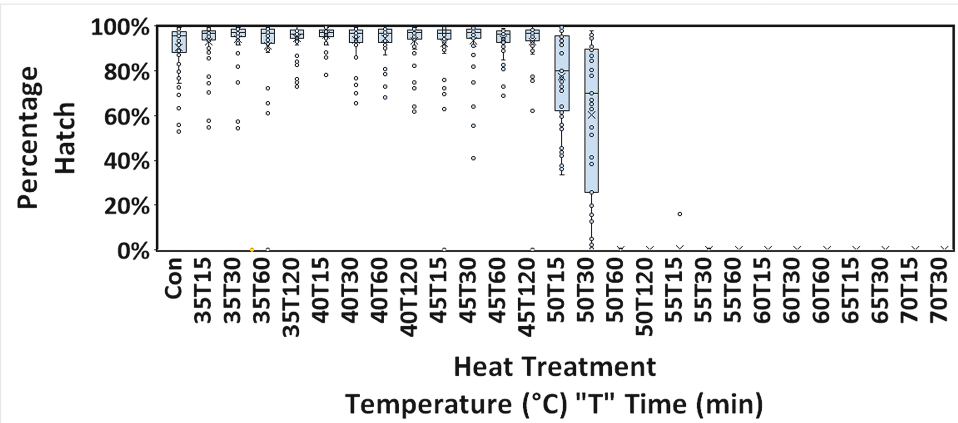

Fig. 1. Percentage hatch of spongy moth eggs at different temperature-time treatments in 2023. Heat treatments are labeled with temperature (°C) "T" duration (min).

Spotted lanternfly egg hatch was inversely correlated with exposure temperatures ≥ 45 °C and duration, while spongy moth egg hatch was inversely correlated with exposure temperatures ≥ 50 °C and duration, indicating that spongy moth eggs are more heat tolerant than spotted lanternfly eggs. Results also suggested that spongy moth eggs may be more vulnerable to treatments in the fall than in the spring, while there was no seasonal difference in spotted lanternfly egg tolerance to heat treatments.

The results of this study may be employed in two types of environmental heating strategies to manage invasive insect hatch. First, heat treatment of forest and agricultural products is a common means of destroying species like spongy moth and spotted lanternfly which are dispersed by human-aided means when products are transferred to new locations. Thus, the results of this study could easily be used to update existing treatments or to incorporate new treatments into APHIS program manuals for spongy moth and spotted lanternfly. In the spongy moth manuel Appendix D both heat treatment and kiln sterilization are mentioned as mitigation options and Appendix F provides temperatures and durations for ensuring eggs in bark compost piles are killed; both could be revised to incorporate our thermal data for killing eggs (USDA APHIS 2019). In the spotted lanternfly environmental assessment high pressure water spray is recommended for removal of eggs and it could potentially be revised to incorporate a temperature requirement to kill the eggs as they are being removed (USDA APHIS 2023). Second, these results suggest that heating from prescribed burning may be suitable for reducing invasive insect eggs in forest or agricultural settings where prescribed burning is acceptable, with minimal damage to tree species. Spotted lanternfly and spongy moth temperature susceptibilities are slightly lower than that of the cambium of tree species (approximately 60 °C), which is also protected by bark that can allow trees to withstand the effects of prescribed fires. For instance, above-canopy air temperatures have been observed to exceed 45 to 50 °C in high intensity prescribed burns, with instantaneous temperatures briefly reaching 332 °C (Clark et al. 2024). Although not described, below-canopy temperatures where invasive insects lay eggs would have experienced substantially higher temperatures. Other data collected illustrate that temperatures during low-intensity prescribed burns may also far exceed those that are lethal to invasive insect eggs but may also be vertically and horizontally variable (Clark et al. 2023). However, this variability in fire effects is managed through ignition patterns and selection of conditions during prescribed burns and can be simulated through new, physics-based prescribed fire simulation tools that can identify the conditions required to achieve desired canopy heating treatments (Bonner et al. 2024). Future research can support these strategies by exploring the effects of prescribed fire heat treatments on invasive insect eggs in outdoor settings.

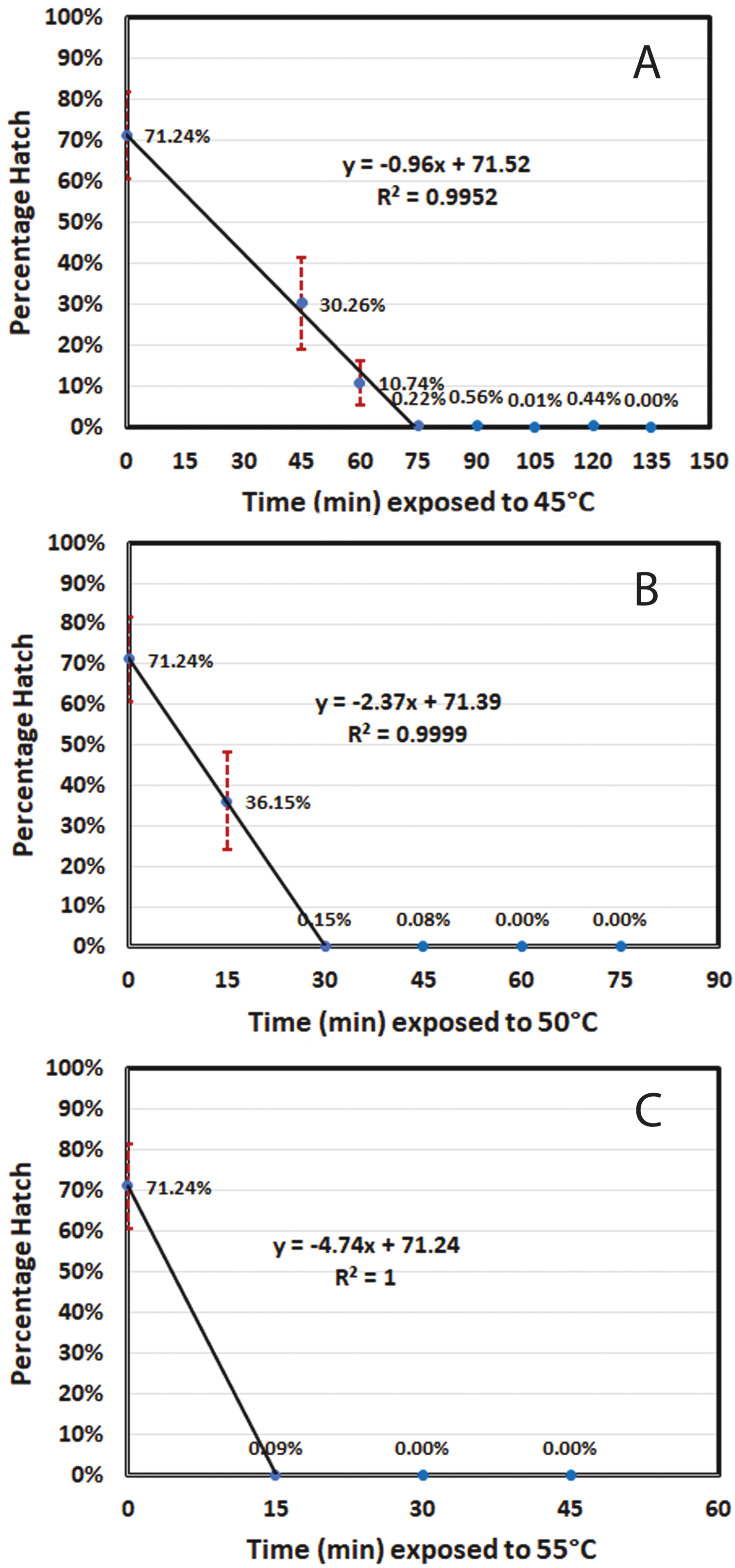

Fig. 2. Percentage hatch of spotted lanternfly eggs at different time treatments at 45 °C (A), 50 °C (B), and 55 °C (C) in 2024.

The differences in heat tolerance between the species may be due to the embryonation stage at which they diapause. Spotted lanternfly eggs enter diapause after some development when they reach the blastokinesis stage (Shim and Lee 2015), which can be reached after a week at 20 °C (Keena and Nielsen 2021), while spongy moth eggs diapause as mature embryonic larvae within the egg (Leonard 1968). Since the spongy moth is in a later embryonic stage, it may be better able to deal with heat stress

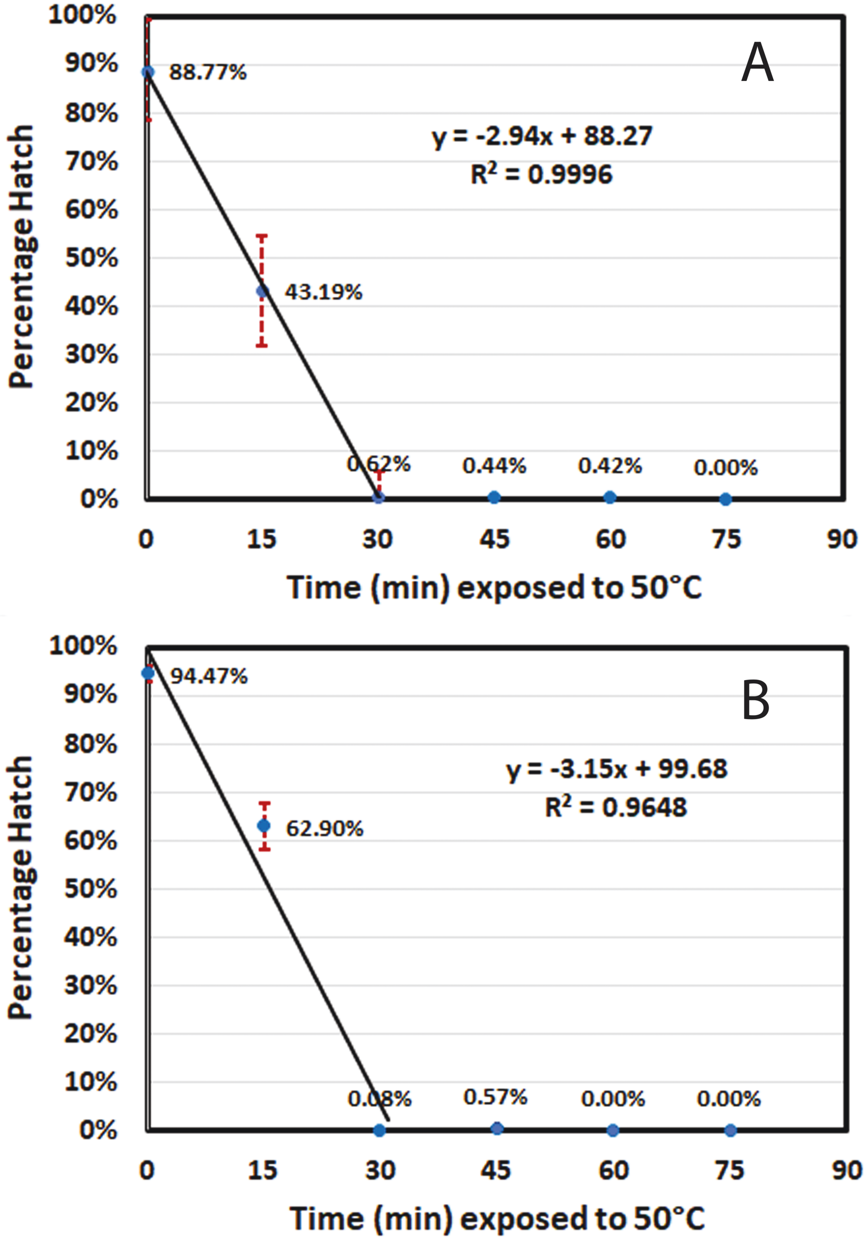

Fig. 3. Percentage hatch of spongy moth eggs at different time treatments at 50 °C in fall (A) and spring (B) in 2024.

which may explain its higher heat tolerance compared to spotted lanternfly.

The seasonal differences in observed response to the heat treatments in only spongy moth and not spotted lanternfly may be due to differences in the eggs' phase during the spring treatments. Spongy moth eggs hatch earlier in the spring than spotted lanternfly eggs when held under the same conditions, so the spongy moth eggs were likely into post-diapause and more responsive to warm temperatures (Gray et al. 1995). Therefore, the short exposure to heat may have caused more of the energy reserves in the eggs to be consumed and put the eggs at risk of running out of energy before conditions were appropriate for hatch. This would not have been the case for the spotted lanternfly eggs, which had only just started accumulating heat above the lower threshold of 7.39 °C in the alternating regime (high 8 to 10 °C and low −1 to −2 °C) when they received the spring treatments so had not moved into active development and were therefore at the same embryonic stage as in the fall.

Treatment variables other than temperature and duration can also impact effectiveness, such as treatment substrate, humidity, oxygen concentration, evenness of heating, rate of heating, and final temperature (Wang et al. 2009). The thickness of the bark on which the spotted lanternfly egg masses were placed was measured to see if there were signs of an effect on treatments. In a few cases of extreme temperatures, the egg masses that were able to hatch tended to be on thicker bark. The type of substrate and its thickness might affect the amount of heat eggs receive. This should be further evaluated, especially since both insect species will lay on many different substrates, which could affect the duration or temperature required to kill all eggs. The rate of temperature increases as the chamber warmed to the set point and treatment timers were started was also tracked. The recorded rates were generally within the normal heating rates (0.067

to 6.25°C/min) used for disinfestation of agricultural commodities (Ikediala et al. 2000), although some were much slower. It is unknown what impact this may have had on the treatments, but the percentage hatch did seem to be affected in the same way in both years despite slower heating rates in the first year. Both factors warrant further evaluation, especially if regulatory treatments are to be developed.

In the first year of study, the spotted lanternfly egg masses did not hatch well, even in the control group. There are several possible reasons for this. First, when the egg masses arrived in the lab, they were placed directly into the alternating regime, so the embryo might not have been given enough time to develop completely. Second, after treatment in March, they were moved to 25 °C, so some of the eggs may not have completed diapause by that time and would not be able to complete it at 25 °C, resulting in egg mortality. The last reason may be the sites from which the egg masses were collected. In some sites, the spotted lanternfly population was in decline, which could have affected egg viability. To address the abovementioned issues, methods were adjusted for 2024, and egg masses were only collected from populations that were on the increase. The egg masses that arrived at the lab from collection sites were held at 20 °C for at least 2 wk before moving to the alternating regime to ensure embryonation was completed. After treatment in March, the egg masses were returned to the alternating regime instead of moving them to 25 °C, to allow normal diapause completion, as fluctuating temperatures are known to better reflect natural conditions than constant temperatures (Colinet et al. 2015). Finally, only vigorous populations of spotted lanternfly were selected for egg mass collection.

The lethal zone for stored products pests starts at 45 °C, and insect death can occur in hours in this zone, depending on the species and stage of development, while insects will die in minutes in temperatures between 50 °C and 60 °C (Fields 1992). For post-harvest insect pests of agricultural products there are several examples of heat treatments. *Tuta absoluta* (Lepidoptera: Gelechiidae) egg hatch was significantly reduced when the eggs were exposed to 44 °C for more than 6 h (Zhou et al. 2024), a 25-min heat treatment at 47 °C will kill 100% of the most tolerant larval stage of codling moth *Cydia pomonella* L. (Chervin et al. 1997), and the eggs of the Mexican fruit fly *Anastrepha ludens* Loew (Diptera: Tephritidae) were all killed when exposed to 50 °C at the air pressure of 150 MPa for 10 min (Velazquez et al. 2010). In general, temperatures between 38 and 54.4 °C, treatment times of up to 12 h, and heating rates between 0.067 and 6.25 °C/min have been reported for disinfestation of agricultural commodities (Ikediala et al. 2000). The temperatures and durations needed to kill the eggs of both species in this study generally fall within the ranges reported for these types of insects, but spongy moth eggs may be more heat tolerant than some other insects.

Heat treatments used for interstate firewood movement vary among U.S. states, from 56 °C for 30 min to 71.1 °C for 75 min. The current International Standards for Phytosanitary Measures (ISPM) No. 15 requires heating solid wood packaging material throughout the profile of the wood for at least 30 min at 56 °C using a conventional kiln and dielectric heating to kill most bark- and wood-boring insects it may contain to significantly reduce the risk of introduction to other countries (FAO 2019). ISPM 15 conditions may be useful for killing the eggs of spotted lanternflies and spongy moths on substrates since there was no hatch at temperatures ≥55 °C for durations longer than 15 min. If eggs of either species are laid on ISPM certified solid wood packaging material that is left outside, it would need to be treated again to kill those eggs. Also, the actual surface temperature when ISPM 15 treatment is applied would likely be much higher since kiln temperatures used range from 60 to 75°C (Haack and Petrice 2022). Firewood treatments may also be effective at killing the eggs of these two species. Future work trying these schedules in a semi-commercial setting using eggs of these insects laid on different substrates is planned to confirm this. Being able to use the same heat treatment regimes as those already in use for other purposes would be convenient; however, knowing the lowest temperatures and durations that will kill the eggs may be more useful if the substrates to be treated are liable to damage by higher temperatures. Additional research done in a closer to operational setting is needed to develop protocols for killing eggs of spotted lanternfly and spongy moth and to determine if the size and type of substrate effects the surface temperature needed to kill the eggs. Some examples of the items that could be heat-treated to kill these insects' eggs are lumber, firewood, solid wood packaging materials, and metal and stone products. Heat treatments may be a viable ecologically friendly method to kill insects that are on vehicles or their cargo, which would help prevent further spread through human-aided means.

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Author contributions

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