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Effects of temperature on the survival of spotted lanternfly active life stages when held without food

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Abstract

1. Spotted lanternfly, *Lycorma delicatula* White (Hemiptera: Fulgoridae), is an invasive Southeast Asian planthopper that was recently introduced into the eastern United States and spreads along human transportation corridors by 'hitch-hiking' on vehicles and cargo.
2. To better understand the risk of establishment when mobile life stages are moved, it is critical to know how long spotted lanternfly mobile life stages will survive without food and water under different temperatures.
3. This work reports on spotted lanternfly first, second, and third instar nymphal and adult survival without food over the 10–30°C temperature range. Survival time without food declined exponentially as temperature increased for all life stages of spotted lanternfly that were evaluated.
4. At temperatures <30°C, first instar nymphs survived longer than second or third instar individuals. Female adults survived about 1 day longer than male adults at all but 10 and 25°C.
5. Without food, 99% of all adults of both sexes are predicted to be dead in less than a week over the temperature range evaluated. First instars, which were the smallest, survived the longest and their survival exponentially decreased as temperature increased.
6. This suggests that more attention to first instar movement may be warranted. The data presented here will provide a basis for assessing the risk of survival of transported spotted lanternfly active life stages along various pathways.

KEYWORDS
adults, nymphs, spotted lanternfly, survival, temperature

INTRODUCTION

Adequate food and water are critical to an insect's survival. Food shortage is a naturally occurring environmental stressor that insects face. The ability to survive chronic or acute food shortage is known as starvation resistance (Hoffmann & Harshman, 1999). Water availability and loss (desiccation) are also environmental factors that affect insect survival. The ability to survive chronic or acute water loss is known as desiccation resistance. Both desiccation and starvation resistance play a role in determining how long an insect in an active stage can survive when held without food.

Many non-native and invasive insects are inadvertently transported by humans in vehicles or on cargo to new potential habitats

without a food or water source being present. When they arrive at the new location, they may have died during transport or have limited time to find food and water before they exhaust their energy reserves. To determine the risk of active stages surviving transport and being able to establish in the new area, it is critical to know how long different active life stages of an insect may survive without food or water at different temperatures. Understanding the effects of the temperature on their survival during transport may also help in identifying protocols that could be put in place to prevent them from arriving alive when associated with cargo.

Spotted lanternfly, *Lycorma delicatula* White, is an invasive Southeast Asian planthopper that was recently introduced into the eastern United States (Dara et al., 2015). Spotted lanternfly is a voracious feeder and can reduce plant resources by both direct feeding and indirectly contributing to a reduction in photosynthesis through sooty mould growth on the honeydew it deposits as it feeds (Lavely et al., 2022; Urban, 2019). It has caused severe damage to vineyards in Pennsylvania and is a nuisance to several other agricultural crops and in residential areas (Harner et al., 2022). Despite state-issued regulations that prohibit movement of any live spotted lanternfly stage or material that might potentially harbour spotted lanternfly outside the quarantine area, it has continued to spread within and between states at an average rate of 38–46 km/year (Cook et al., 2021). Much of the dispersal appears to be shorter distances caused by natural dispersal, but there have also been longer distance jumps ranging from 55 to 92 km/year that are most likely attributable to spotted lanternfly moving by human-aided means (Cook et al., 2021). Another study has found that human-aided movement is a very important factor in determining the spread of this insect and that its spread follows human transport corridors (Ladin et al., 2023). These long-distance movements are thought to primarily occur when eggs are laid on vehicles (trains, cars, etc.) or cargo that was stored outdoors before transport. However, this insect can also move when mobile life stages 'hitch-hike' in vehicles or their cargo. Without preventative management, spotted lanternfly is predicted to reach California, a major grape growing area, by 2033 (Jones et al., 2022) and maximum entropy modelling of the spotted lanternfly niche based on occurrence information has predicted it has the potential to establish in the East, central and Pacific sections of the United States (Wakie et al., 2020).

There is information on spotted lanternfly thermal tolerances for development and survival when held with food (Kreitman et al., 2021), but no information on survival without food at different temperatures. To better understand the risk of establishment when mobile life stages are moved, it is critical to know how long spotted lanternfly mobile life stages will survive without food and water under different temperatures. Different mobile stages have the potential to be moved at different times of year and under different temperature conditions and that may impact their survival (both desiccation and starvation resistance) and whether they will arrive alive and with enough remaining energy to find food and establish in the new location. This work reports on spotted lanternfly first, second and third instar nymphal and adult survival without food over the 10–30°C temperature range. Implications of the results for regulatory purposes will be discussed.

MATERIALS AND METHODS

Individuals used in the study

Nymphs that were used came from 12 geographically distinct populations collected as egg masses in fall 2021, and the adults were all collected from one location in September 2022 (Table 1). Nymphs were sourced from several different populations to capture the full range of variability in thermal tolerance since it has been shown to vary between populations (Keena et al., 2023). Adults were collected about 1.5 months after the first adult was observed and shortly before the first egg masses were seen at the site. The spotted lanternfly egg masses were brought to the USDA Forest Service Quarantine Laboratory, Ansonia, CT, under valid state and federal permits. The timing of egg mass collection was chosen to ensure that the eggs had been laid within the last 2 weeks (most within a couple of days). The egg masses were collected and held at 15°C until hatch as described in Keena and Nielsen (2021). Nymphs from six to seven of these populations were used for each of the instar trials. Newly hatched first instars were used for the study, and additional first instars from the populations (10–15 from each egg mass) were reared to the beginning of the required instar in large 60 × 60 × 120 cm (BugDorm 6S620, MegaView Science Co., Ltd, Taichung, Taiwan) mesh cages with clear front and back that contained both *Ailanthus altisima* (tree of heaven) saplings and *Vitis labrusca* (concord grape) vines. The cages with nymphs to be used for the second and third instar part of the study were held at room temperature (~20°C), ambient humidity (~60% relative humidity [RH] that time of year) and the lights were kept on in the room.

Treatments and data collection

Containers of nymphs (first, second or third instars) or adults were placed at each of the following constant temperatures: 10, 15, 20, 25 and 30°C. The only exception was that no second instar nymphs were held at 10°C. The environmental chambers typically remained within 1°C of the set point. RH was passively maintained using open buckets (with 896 cm^2 of surface area) of water in the bottom of all but two chambers. Two chambers (15 and 25°C) had full humidity controls and did not require an open water source. The humidity in the chambers averaged 85 ± 15 at 10°C, 65 ± 2 at 15°C, 80 ± 5 at 20°C, 60 ± 5 at 25°C and 45 ± 5% RH at 30°C. Humidity and temperature data were recorded using chart recorders. The light:dark cycle in all the chambers was set at LD 14:10 h.

Ten first instar nymphs that hatched the same day, from more than one egg mass of the same population, were placed in a 60 × 15 mm vented Petri dish and held at one of five temperatures. A total of 180 first instar nymphs (18 dishes) were held at each temperature. Second and third instar nymphs from the same population that were 24–48 h post-moult were held five to a 60 × 15 mm Petri dish. A total of 90-second instar nymphs (18 dishes) and 115 third instar nymphs (23 dishes) were held at each temperature. Numbers of

TABLE 1 Approximate location (latitude and longitude) of source populations of *Lycorma delicatula* used in this study.

Population code	State	Closest city	Latitude	Longitude	Collection date	Stage collected	Stage used (*n*)
NDE	DE	New Castle	39.69° N	75.58° W	12 October 2021	35 egg masses	3rd instars (100)
OCT	CT	Orange	41.28° N	73.05° W	20 October 2021	46 egg masses	1st (100) and 2nd instars (45)
CCT	CT	Cheshire	41.53° N	72.93° W	15 November 2021	40 egg masses	2nd instars (35)
FCT	CT	Fairfield	41.14° N	73.29° W	21 September 2022	99 adults	Adults (99)
SMD	MD	Cardiff	39.61° N	76.16° W	13 October 2021	71 egg masses	1st (150) and 3rd instars (100)
RNJ	NJ	National Park	39.87° N	75.19° W	12 October 2021	77 egg masses	1st (150) and 2nd instars (95)
SNJ	NJ	High Bridge	40.66° N	74.93° W	27 October 2021	75 egg masses	1st (150) and 3rd instars (75)
GNY	NY	Staten Island	40.55° N	74.12° W	7 October 2021	67 egg masses	1st (150), 2nd, (60) and 3rd instars (100)
BPA	PA	Brownsville	40.38° N	76.06° W	27 October 2021	60 egg masses	1st (150) and 2nd instars (50)
HPA	PA	Harrisburg	40.29° N	76.89° W	13 October 2021	88 egg masses	3rd instars (100)
MPA	PA	Manor	40.33° N	79.67° W	3 November 2021	11 egg masses	2nd instars (75)
PPA	PA	Pittsburgh	40.43° N	80.00° W	3 November 2021	61 egg masses	3rd instars (100)
WVA	VA	Winchester	39.21° N	78.16° W	25 October 2021	57 egg masses	1st instar (50)

dishes per temperature of nymphs from each population were kept the same, but there were more dishes from some populations than others based on how many nymphs were available from each population (see Table 1 for numbers of nymphs from each population). The field-collected adults were sexed and held singly in 237 mL unwaxed paper drinking cups with a mesh lid held on by a rubber band. This was necessary to prevent adults from damaging each other and provide them with adequate airflow to survive. Eight to nine males and 11–13 females were held in each temperature, and the only exception was 30°C where there were 3 males and 15 females. The individuals in the containers were checked daily, and the dead were counted. Survival time for each individual was calculated in days.

Statistical analysis

Individual survival time in days was analysed using a generalized linear mixed model (PROC GLIMMIX, SAS Institute, 2015). The survival time data were not normally distributed and fitted to a gamma distribution with a log link because the data fit this distribution the best of those that were evaluated using an Anderson–Darling test. The data for the first three instars were analysed together to make comparisons between instars possible and the models included temperature, instar and the interaction between the two. Population nested within the dish was used as a random effect for the nymphal model. The model for the adults included temperature, sex and the interaction between the two. The Tukey–Kramer post hoc analysis at $\alpha = 0.05$ was used to determine if the means were significantly different. The residuals for each model were used to test the relationship for normality, and Levene's test was used to check the homogeneity of treatment variance. Exponential curves (survival time [days] $= a^{*}\exp^{\text{Temperature}^{*}b}$) were fitted to the relationship between temperature and individual survival time using a non-linear regression model (SAS PROC NLIN, SAS Institute, 2015). In the equation, '*a*' is the estimated maximal survival as temperature nears 0°C and '*b*' is the rate of decline in survival time as temperature increases. These curves will allow for estimates of potential survival at temperatures not evaluated. Kaplan–Meier product limit estimates (Statistix 10, Analytical Software, 2013) of the survival functions were used to calculate the days with 95% confidence intervals that 99, 90, 50 and 10 percentiles of nymphs

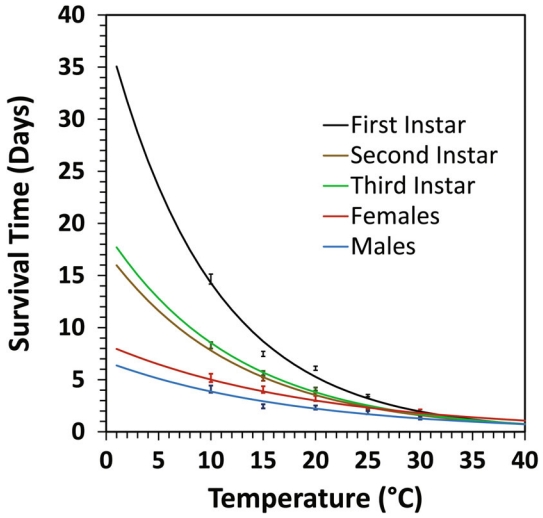

FIGURE 1 Predicted survival time (days) for *Lycorma delicatula* active life stages held at different temperatures (°C) without food. Error bars are the standard error for the average of the individual responses at each temperature which were used in estimating the curves.

TABLE 2 Parameter values for exponential models used to describe the relationship between *Lycorma delicatula* instar/stage survival without food and holding temperature.

Instar/stage	*a*	*b*	Statistics	*n*	$_{Adj}R^2$
First	38.73 ± 0.69	−0.100 ± 0.001	$F = 15235.4$; df = 2, 898; $p < 0.0001$	900	0.9109
Second	17.30 ± 1.27	−0.080 ± 0.004	$F = 1624.9$; df = 2, 358; $p < 0.0001$	360	0.5947
Third	19.19 ± 0.70	−0.081 ± 0.003	$F = 3199.5$; df = 2, 573; $p < 0.0001$	575	0.7244
Adult female	8.37 ± 0.42	−0.051 ± 0.003	$F = 1383.4$; df = 2, 60; $p < 0.0001$	62	0.8464
Adult male	6.73 ± 0.82	−0.055 ± 0.008	$F = 299.8$; df = 2, 35; $p = 0.001$	37	0.6065

Note: Exponential model $Y = a^{*}\exp^{X^{*}b}$. The '*n*' is the number of individual survival data points used.

TABLE 3 Mean [±SE (*n*)] for various *Lycorma delicatula* instar/stage parameters under different temperature regimes.

Instar/stage	Average survival time (days) at set temperatures					Statistics
	10°C	15°C	20°C	25°C	30°C	
First	14.60 ± 0.56a (180)	7.49 ± 0.29b (180)	6.10 ± 0.23c (180)	3.45 ± 0.13e (180)	1.69 ± 0.06g (180)	Temperature * Instar $F = 10.17$; df = 7, 243.7; $p < 0.0001$
Second	NA	5.01 ± 0.21d (90)	3.61 ± 0.15e (90)	2.38 ± 0.10f (90)	1.41 ± 0.06g (90)	
Third	8.32 ± 0.31b (115)	5.63 ± 0.21cd (115)	4.11 ± 0.15e (115)	2.21 ± 0.08f (115)	1.63 ± 0.06g (115)	
Adult female	5.17 ± 0.4a (12)	4.05 ± 0.32b (11)	3.20 ± 0.25b (11)	2.16 ± 0.16cd (13)	2.00 ± 0.15cd (15)	Temperature * Sex $F = 2.83$; df = 4, 88.06; $p = 0.0295$
Adult male	4.10 ± 0.34a (8)	2.45 ± 0.2c (9)	2.33 ± 0.19cd (9)	1.84 ± 0.16de (8)	1.34 ± 0.16e (3)	

Note: Means within a statistical analysis group (nymphs or adults) followed by a different letter are significantly different from each other at $p < 0.05$ using Tukey–Kramer post hoc test (SAS Institute, 2015). Sample size (*n*) is the total number of individuals per temperature.

(by instar) and adults (sexes combined) survived in each of the temperature treatments. These confidence intervals will be useful for managers to assess risks of survival under different conditions since the goal would be no survival during transport.

RESULTS

Survival time without food declined exponentially as temperature increased for all instars and life stages of spotted lanternfly that were evaluated (Figure 1 and Table 2). The effect of temperature on survival differed significantly by life stage and sex in adults (Table 2). Response to temperature was the weakest in adults with only a 3-day difference between survival time at 10 and 30°C and greatest for first instar individuals with a 13-day difference for the same temperature range (Tables 2 and 3). At temperatures <30°C, first instar nymphs survived longer than second or third instar individuals (Tables 2 and 3). Female adults survived longer than male adults at all but 10 and 25°C (Tables 2 and 3). The difference in survival between male and female adults was about 1 day. Adjusted R^2 values for predicted survival curve fits were ≥0.7 for all but the second instar nymphs and adult males (Figure 1). The estimated curves for the second and third instars were very similar.

Without food, 99% of all adults of both sexes are predicted to be dead in less than a week over the temperature range that was evaluated (Table 4). In fact, adults held at 30°C without food all died within the first 2 days. The models predicted that it would take more than 2 weeks for 99% of first and third instar nymphs held at 10°C without food to die. Even at 20°C, it was predicted that it would take longer than a week for 99% of the first instar nymphs to die.

DISCUSSION

Temperature and instar/stage both affected the survival time of the active life stages of spotted lanternfly when held without food. As the temperature increased, survival time decreased. As spotted lanternfly developed and increased in mass, survival time also declined. These models provide good predictors of survival under different temperatures and when taken along with other factors that affect survival during movement can help to predict spotted lanternfly survival without food during human-aided transport.

When spotted lanternfly is held without food, they could suffer from both starvation and desiccation since all their moisture comes from their food. An insect's ability to resist desiccation is determined by the quantity of stored water, the rate of water loss and the lower threshold of water needed for survival (Hoffmann & Harshman, 1999). Water can be lost both through open spiracles and the cuticle. Lower metabolic rates can reduce the time the spiracles need to be open and increased lipids associated with the cuticle can reduce desiccation. Metabolic rate increases exponentially with temperature and scales with the 3/4 power of body mass (Gillooly et al., 2001). Desiccation in general increases with increasing temperature and as surface area to volume ratios increase (smaller sized individuals have higher ratios and less resistance; Hoffmann & Harshman, 1999). So, if the survival of the active life stages of spotted

TABLE 4 The 99, 90, 50 and 10 percentile estimates of the survival time in days (95% confidence intervals) for *Lycorma delicatula* individuals in each instar/stage in each temperature treatment.

		Instar			
Temperature treatment (°C)	Estimated survival percentile	First	Second	Third	Adult
10	10	9.8 (9–11)		1.2 (1–3)	NA
	50	12.0 (11–13)		5.0 (4–6)	3.0 (3–4)
	90	15.0 (14–15)		9.0 (8–9)	5.0 (4–5)
	99	17.0 (16–17)		11.0 (11–13)	6.0 (5–NA)
15	10	3.4 (1–5)	NA	3.0 (3–3)	NA
	50	6.0 (5–6)	3.0 (2–3)	4.0 (3–4)	2.0 (2–2)
	90	8.0 (7–8)	5.0 (5–6)	6.0 (5–6)	3.0 (2–4)
	99	9.0 (9–10)	7.0 (7–8)	7.0 (7–9)	4.0 (4–NA)
20	10	3.4 (1–4)	NA	1.2 (1–2)	NA
	50	5.0 (5–5)	2.0 (2–2)	3.0 (3–3)	2.0 (2–2)
	90	6.0 (6–6)	4.0 (3–4)	4.0 (4–4)	2.0 (2–3)
	99	7.0 (7–8)	5.0 (5–6)	5.0 (5–6)	3.0 (3–NA)
25	10	2.0 (2–2)	NA	1.0 (1–1)	NA
	50	3.0 (2–3)	2.0 (1–2)	1.0 (1–2)	2.0 (1–2)
	90	4.0 (3–4)	2.0 (2–3)	2.0 (2–2)	2.0 (2–2)
	99	4.0 (4–4)	3.0 (3–4)	3.0 (3–3)	2.0 (2–NA)
30	10	1.0 (1–1)	NA	1.0 (1–1)	NA
	50	1.0 (1–1)	1.0 (1–1)	1.0 (1–1)	1.0 (1–2)
	90	2.0 (2–2)	1.0 (1–2)	2.0 (2–2)	2.0 (2–2)
	99	2.0 (2–2)	2.0 (2–2)	2.0 (2–2)	2.0 (2–NA)

Note: Estimates were obtained using the Kaplan–Meier product limit estimates of the survival functions (Analytical Software, 2013). Percentiles that could not be calculated are denoted as NA (not available). Cells in the table that are greyed out are treatment and instar combinations that were not done.

lanternfly simply depended on how fast the individuals would lose body water, then the later instars and adults, which have a lower surface area to volume ratio, would be expected to survive longer, but the opposite was true. However, desiccation resistance also depends on what percentage of body water the individual can tolerate before it becomes lethal. For example, first instar kudzu bugs (*Megacopta cribraria* [Hemiptera: Plataspidae]) held at 30°C and 0%–2% RH were found to tolerate much higher body water loss than adults and later instars (Benk et al., 2020). So, it is possible that desiccation resistance in addition to starvation may have played a role in the mortality for spotted lanternfly active life stages held without food if first instars of this species also can tolerate higher percent water loss than the larger nymphs and adults. The humidities used in this study were generally higher but the somewhat lower % RH in the highest temperature treatment could have contributed some to mortality. More work would be needed to determine how humidity and temperature interact to affect spotted lanternfly survival without food. Care should also be taken when extrapolating these results to the field since laboratory-reared nymphs may differ in water content and resistance to both desiccation and starvation.

Starvation resistance is determined by the quantity and quality (lipid to triglyceride ratio) of energy reserves, the rate of usage of stored energy resources (metabolic rate) and the lower threshold of energy resources needed for survival under starvation (Rion & Kawecki, 2007). If spotted lanternfly starvation resistance is primarily driven by metabolic rates, then higher resistance should be seen for smaller nymphs (early instars compared to later ones) and when the temperature is cooler because metabolic rates would be lower in both cases. For example, the first instars that were the smallest survived the longest and their survival exponentially decreased as temperature increased. The only finding for spotted lanternfly that does not fit this pattern was that adult females lived longer than adult males despite being larger in size, which has also been seen in other laboratory studies (Nixon, Jones, Dechaine, et al., 2022). This difference between the sexes could be due to lipid content differences since females likely build lipid stores for the eggs in the 1–2 months they spend feeding before egg-laying starts (Calvin et al., 2023). Higher lipid to lean body mass ratios in *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) have been shown to increase starvation resistance (Jang & Lee, 2018). Further work would be needed to determine the actual cause of the difference in survival between the sexes. In addition, the adults used in this study were just starting to show the yellow strip along the abdomen (it increases in width as sexual maturation occurs) and were not at full potential weight, so care should be taken in using these results to predict the survival over the entire adult period. The survival of adults at different points in the maturation process leading

up to mating and oviposition should be determined since this is a long time period and their abdominal weight increases, which could also change lipid to lean body mass ratios.

There are other invasive forest insects, whose egg masses and life stages are readily transported on vehicles and cargo. So how do the risks associate with spotted lanternfly human-aided movement compare to these other insects. Spotted lanternfly first instar nymphs survived a shorter time than did spongy moth, *Lymantria dispar* L. (Lepidoptera: Erebidae), first instar caterpillars (Keena & Shi, 2019) when evaluated under the same temperatures. At 10°C, spongy moth survived about a week longer than spotted lanternfly, and at 25–30°C, the caterpillars survived about 2 days longer than the nymphs. The reason for the difference in survival is not known but spongy moth larvae regularly stay on the egg mass for several days before dispersing in nature and tend to hatch earlier than spotted lanternfly (unpublished data) so may have more energy reserves when they hatch compared to spotted lanternfly. Therefore, the risks associated with first instar spotted lanternfly human-aided movement may be lower than those associated with spongy moth first instars.

Not all the individual nymphs died at the same time so there was some variation in starvation resistance. The variation in survival time was most pronounced at the cooler temperatures. In *D. melanogaster*, starvation resistance varies clinally across latitudes; cold-adapted individuals have higher mass-specific metabolic rates to maintain growth in cooler climates (Jang & Lee, 2018). This makes the cold-adapted individuals more susceptible to starvation because of higher energy expenditures. The spotted lanternfly nymphs used in this study were sourced from several different populations located in different plant cold hardiness zones. Previous work has shown spotted lanternfly may be adapted to different climates (Keena et al., 2023) so this could be playing a role in the differences seen in survival time within an instar and temperature combination. This should also be considered when developing risk models for nymphs that travel by human-aided means since the source climate where nymphs come from may play a role in survival time.

This study is a worst-case scenario since individual spotted lanternfly nymphs and adults were not considered dead until they could not move a leg. Individuals were generally unable to walk a day or more before they were considered dead so they would likely not be able to hold onto a plant and feed to regain their strength when exposed to shorter durations without food. Also, the humidities used in the study may be much higher than an insect would be exposed to in a vehicle or cargo so the effects of desiccation combined with starvation would be extenuated. So, using these survival durations provided here should be good upper limits for this insect.

First instar nymphs would normally be present on the landscape when temperatures are ≤20°C in the spring. Later instars would naturally be exposed to higher temperatures since they would be present in the late spring or early summer. However, if nymphs end up in a vehicle or on cargo, they may be exposed to temperatures they would normally not be exposed to in nature, so having the data that will predict their survival over a broader temperature range is important to understanding the risks associated with human-aided movement. Adults in nature may be exposed to the full range of temperatures evaluated since they first appear during the summer but live into the fall until freezing temperatures kill them or they die of old age in warmer climates.

From a regulatory perspective, the good news is that adults who are transported without food for longer distances (takes multiple days) or at higher temperatures are not likely to survive long enough to find food in a new location. The bad news is that first instars can survive much longer than adults and the later instars. So, if first instars are transported soon after hatch or egg masses hatch during transport, the first instar individuals may have several days to find food in the new location. First instars also have a broader host range, which will give them a greater chance of finding acceptable food and establishing (Nixon et al., 2023; Nixon, Jones, Tang, et al., 2022). However, first instars do not disperse very far very fast, on average about 6 m in 10 days in a forested setting (Keller et al., 2020), so proximity to food at the release point will be important. In addition, enough individual first instars would have to be transported to or hatch at the same location so that once they become adults, they could find a mate. If the right circumstances exist, transporting first instars could be riskier than transporting later instars or virgin female adults. Obviously, if a mated female survives transport to a new location and can successfully oviposit that would pose a higher risk of establishment. Most of the regulator's attention has been given to watching for and stopping adult and egg mass movement by humans but first instar movement should not be ignored since they may pose an additional risk that has been overlooked. The data presented here will provide a basis for assessing the risk of survival of transported spotted lanternfly active life stages along various pathways and could potentially be used to find safer transport protocols for cargo that may be infested.

AUTHOR CONTRIBUTIONS

Melody Keena: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; supervision; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The original data is available on request from the author.

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REFERENCES

Analytical Software. (2013) *Statistix 10 user's manual*. Tallahassee, FL: Analytical Software.

Benk, G., Thompson, P.J., Hu, X.P. & Appel, A.G. (2020) Water loss and desiccation tolerance of the two yearly generations of adult and nymphal kudzu bugs, *Megacopta cribraria* (Hemiptera: Plataspidae). *Environmental Entomology*, 49, 651–659.

Calvin, D.C., Rost, J., Keller, J., Crawford, S., Walsh, B., Bosold, M. et al. (2023) Seasonal activity of spotted lanternfly (Hemiptera: Fulgoridae), in Southeast Pennsylvania. *Environmental Entomology*, 52, 1108-1125. Available from: https://doi.org/10.1093/ee/nvad093 (online early).

Cook, R.T., Ward, S.F., Liebhold, A.M. & Fei, S.L. (2021) Spatial dynamics of spotted lanternfly, *Lycorma delicatula*, invasion of the Northeastern United States. *NeoBiota*, 70, 23–42.

Dara, S.K., Barringer, L. & Arthurs, S.P. (2015) *Lycorma delicatula* (Hemiptera: Fulgoridae): a new invasive pest in the United States. *Journal of Integrated Pest Management*, 6. Available from: https://doi.org/10.1093/jipm/pmv021

Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M. & Charnov, E.L. (2001) Effects of size and temperature on metabolic rate. *Science*, 293, 2248–2251.

Harner, A.D., Leach, H.L., Briggs, L. & Centinari, M. (2022) Prolonged phloem feeding by the spotted lanternfly, an invasive planthopper, alters resource allocation and inhibits gas exchange in grapevines. *Plant Direct*, 6, e452. Available from: https://doi.org/10.1002/pld3.452

Hoffmann, A.A. & Harshman, L.G. (1999) Desiccation and starvation resistance in *Drosophila*: patterns of variation at the species, population and intrapopulation levels. *Heredity*, 83, 637–643.

Jang, T. & Lee, K.P. (2018) Context-dependent effects of temperature on starvation resistance in *Drosophila melanogaster*: mechanisms and ecological implications. *Journal of Insect Physiology*, 110, 6–12.

Jones, C., Skrip, M.M., Seliger, B.J., Jones, S., Wakie, T., Takeuchi, Y. et al. (2022) Spotted lanternfly predicted to establish in California by 2033 without preventative management. *Communications Biology*, 5, 558. Available from: https://doi.org/10.1038/s42003-022-03447-0

Keena, M.A., Hamilton, G. & Kreitman, D. (2023) The potential climatic range of spotted lanternfly may be broader than previously predicted. *Frontiers in Insect Science*, 3. Available from: https://doi.org/10.3389/finsc.2023.1092189

Keena, M.A. & Nielsen, A.L. (2021) Comparison of the hatch of newly laid *Lycorma delicatula* (Hemiptera: Fulgoridae) eggs from the United States after exposure to different temperatures and durations of low temperature. *Environmental Entomology*, 50, 410–417.

Keena, M.A. & Shi, J. (2019) Effects of temperature on first instar *Lymantria* (Lepidoptera: Erebidae) survival and development with and without food. *Environmental Entomology*, 48, 655–666.

Keller, J.A., Johnson, A.E., Uyi, O., Wurzbacher, S., Long, D. & Hoover, K. (2020) Dispersal of *Lycorma delicatula* (Hemiptera: Fulgoridae) nymphs through contiguous, deciduous forest. *Environmental Entomology*, 49, 1012–1018.

Kreitman, D., Keena, M.A., Nielsen, A.L. & Hamilton, G. (2021) Effects of temperature on development and survival of nymphal *Lycorma delicatula* (Hemiptera: Fulgoridae). *Environmental Entomology*, 50, 183–191.

Ladin, Z.S., Eggen, D.A., Trammell, T.L.E. & D'Amico, V. (2023) Human-mediated dispersal drives the spread of the spotted lanternfly (*Lycorma delicatula*). *Scientific Reports*, 13, 1098. Available from: https://doi.org/10.1038/s41598-022-25989-3

Lavely, E., Iavorivska, L., Uyi, O., Eissenstat, D.M., Walsh, B., Primka, E.J. et al. (2022) Impacts of short-term feeding by spotted lanternfly (*Lycorma delicatula*) on ecophysiology of young hardwood trees in a common garden. *Frontiers in Insect Science*, 2. Available from: https://doi.org/10.3389/finsc.2022.1080124

Nixon, L.J., Barnes, C. & Leskey, T.C. (2023) Assessing acceptability of wild and cultivated hosts of *Lycorma delicatula* (Hemiptera: Fulgoridae) under semifield conditions. *Environmental Entomology*, 52, 879–887. Available from: https://doi.org/10.1093/ee/nvad078

Nixon, L.J., Jones, S., Dechaine, A.C., Ludwick, D., Hickin, M., Sullivan, L. et al. (2022) Development of rearing methodology for the invasive spotted lanternfly, *Lycorma delicatula* (Hemiptera: Fulgoridae). *Frontiers in Insect Science*, 2, 1025193. Available from: https://doi.org/10.3389/finsc.2022.1025193

Nixon, L.J., Jones, S.K., Tang, L., Urban, J., Felton, K. & Leskey, T.C. (2022) Survivorship and development of the invasive *Lycorma delicatula* (Hemiptera: Fulgoridae) on wild and cultivated temperate host plants. *Environmental Entomology*, 51, 222–228.

Rion, S. & Kawecki, T.J. (2007) Evolutionary biology of starvation resistance: what we have learned from *Drosophila*. *Journal of Evolutionary Biology*, 20, 1655–1664.

SAS Institute. (2015) *SAS/STAT user's guide, version 9.4*. Cary, NC: SAS Institute.

Urban, J.M. (2019) Perspective: shedding light on spotted lanternfly impacts in the USA. *Pest Management Science*, 76, 10–17.

Wakie, T.T., Neven, L.G., Yee, W.L. & Lu, Z.Z. (2020) The establishment risk of *Lycorma delicatula* (Hemiptera: Fulgoridae) in the United States and globally. *Journal of Economic Entomology*, 113, 306–314.

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