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SYMPOSIUM

Invasive Spotted Lanternflies (*Lycorma delicatula*) Are Larger in More Urban Areas

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Synopsis Urbanization promotes the formation of heat islands. For ectothermic animals in cities, the urban heat island effect can increase developmental rate and result in smaller adult body size (i.e., the temperature-size rule). A smaller adult body size could be consequential for invasive urban ectotherms due to potential effects of body size on thermal tolerance, dispersal distance, and fecundity. Here, we explored the effect of urbanization on body size in the spotted lanternfly (*Lycorma delicatula*), an invasive planthopper (Hemiptera: Fulgoridae) that is rapidly spreading across urban and non-urban settings in the United States. We then evaluated the consequences of spotted lanternfly body size for heat tolerance, a trait with importance for ectotherm survival in urban heat islands. Contrary to our expectations, we found that both male ($P = 0.011$) and female ($P < 0.001$) spotted lanternflies were larger in more urbanized areas and that females displayed a positive effect of body size on resistance to hot temperatures ($P = 0.018$). These results reject plasticity in developmental rate due to the urban heat island effect as an explanation for spotted lanternfly body size and instead lend necessary (but insufficient) support to an adaptive explanation stemming from advantages of larger body size in cities. This study demonstrates a positive effect of urbanization on spotted lanternfly body size, with potential implications for dispersal distance, fecundity, and thermal tolerance in urban areas.

Introduction

Urbanization is progressing at an unprecedented rate, with global urban extent expanding by >9500 km^2 per year (Liu et al. 2020). While cities have many unique characteristics that differentiate them from natural areas, one that stands out is the presence of human-made surfaces (e.g., buildings, roads, asphalt, and other impervious surfaces) that store heat (Chen et al. 2023). For this reason, there is a high correlation between the prevalence of impervious surface and land surface temperature (Imhoff et al. 2010; Ezimand et al. 2024). Combined with corresponding vegetation loss and anthropogenic heat production (Mohajerani et al. 2017), cities thus promote the formation of “urban heat islands,” with daytime temperatures that can be 8°C higher than surrounding rural areas (Imhoff et al. 2010), and they contain hotspots of extreme surface temperatures (Mentaschi et al. 2022). Urban heat islands subsequently affect the ecology and evolution of species inhabiting these thermal environments, with particular importance for ectothermic animals for which body temperature is closely tied to that of the environment (e.g., Angiletta et al. 2007; Brans et al. 2017).

We focus here on the effect of urban conditions on ectotherm body size, a trait with significant implications for ecology, physiology, and fitness (Chown and Gaston 2010) as well as community and ecosystem dynamics (Lövei and Magura 2022). In ectotherms, body size is related to developmental temperature via the temperature-size rule, which states that developmental rate is correlated with temperature and that accelerated development results in smaller adult body size (Atkinson 1994; Angiletta and Dunham 2003). It follows that, in the absence of selection for larger body size, ectotherms are expected to be smaller in cities due to the thermal environment (Merckx et al. 2018). Smaller

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ectotherm body size can then impact heat tolerance (e.g., Baudier and O'Donnell 2018) and rates of evaporative water loss (e.g., Kühsel et al. 2016), two traits with consequences for survival in urban heat islands.

The relationship between the thermal environments of cities and ectotherm body size may be of particular importance for the success of invasive insects. Cities often play a key role in the introduction of invasive species (Borden and Flory 2021), with the establishment of invasive insects facilitated in large part by the prevalence of non-native plant species in urban areas (Branco et al. 2019). However, if the urban heat island effect causes smaller adult body sizes in invasive insects, this could affect the ability of invasive insects to survive the hotter environmental temperatures of cities. Furthermore, smaller adult body size also has the potential to reduce the dispersal capacity, mate-finding abilities, and fecundity of invasive insects (Kajita and Evans 2010; Hemptinne et al. 2012), such that cities could act as ecological traps for these species (Zuniga-Palacios et al. 2021; Frank and Cowper 2022).

Here, we studied the relationship between urbanization and body size in the spotted lanternfly (*L. delicatula*), a recently introduced invasive insect in the United States (Barringer et al. 2015) that is rapidly spreading across urban and non-urban environments to test two hypotheses: (1) Body size has an inverse relationship to percent impervious surface; and (2) Body size affects heat tolerance. Contrary to our expectations stemming from the temperature-size rule, we found that spotted lanternflies in cities were larger than those in less urban areas and that larger females are more resistant to hot temperatures. These results lend necessary but insufficient support to an adaptive explanation for spotted lanternfly body size rather than one based on the effect of urban heat islands on plasticity in developmental rate.

Materials and methods

Study organism

The spotted lanternfly (*L. delicatula*) is a polyphagous planthopper (Hemiptera: Fulgoridae) that is native to China (Chu 1930). An invasive population of spotted lanternfly was first detected in the USA in Berks County, Pennsylvania, in 2014 (Barringer et al. 2015). Since its introduction, the species has rapidly expanded its range (Cook et al. 2021), establishing populations in 17 US states (USDA APHIS n.d.). This species thrives in a diverse array of habitats, with populations present in urban and non-urban settings, possibly due to its broad diet and ontogenetic shifts in host preference (Urban et al. 2021). The spotted lanternfly represents a major economic threat in the United States (Urban 2019; Urban and Leach 2023), with particular concern for agriculture.

Sample collection and body size measurements

We collected 2405 adult spotted lanternflies (980 males; 1425 females) from 93 locations in New Jersey, USA, in September and October of 2021 (Fig. 1). Collection sites represented a variety of habitats, ranging from rural to highly urbanized settings. At each site, we collected spotted lanternflies by hand and placed them in labeled plastic bags with other individuals from the same sample site and collection date. We then stored the bags in a −20°C freezer to euthanize the animals and preserve their tissue for analyses. We recorded the date and geographic coordinates (via Google Maps) of each sampling event.

The number of samples collected per site ranged from 1 to 215 ($x = 25.86 \pm 35.03$), but there were robust sample sizes across the urbanization gradient. For example, 436 females were collected from the most urban areas ($\geq$50% mean impervious surface), whereas 390 females were collected from the most rural areas ($\leq$15% mean impervious surface). Likewise, 329 males were collected from the most urban areas, and 117 males were collected from the most rural areas.

From January to April of 2024, we thawed each sample for approximately 20 min at room temperature. We determined the sex of each individual by noting the presence or absence of red valvifers at the posterior end of the abdomen and inspected the wings to ensure that they were intact. We then used stainless steel digital calipers (VWR® cat. 62379-531) to measure total body length, a metric of body size, as the distance from the tip of the head to the tip of the folded wings (Baker et al. 2019). We did not measure the weight of these individuals since they had been frozen and subject to desiccation for approximately 2 years.

Quantifying urbanization and altitude

We quantified the degree of urbanization of each sample site by calculating the mean percent impervious surface within a 5-km buffer around each site (Fig. 1). To do so, we used ArcGIS Pro v. 3.3 (Esri) to plot the coordinates of each sample site on the impervious surface layer of the 2021 National Land Cover Database of the United States (Dewitz 2023). We then constructed 5-km radius buffers around each site and used the Zonal Statistics Geoprocessing Tool to calculate the mean percent impervious surface within each buffer. A 5-km radius buffer was selected because spotted lanternflies can disperse 3–4 miles (i.e., 5–6.4 km) during their lifespan (Cornell University n.d.). Mean percent

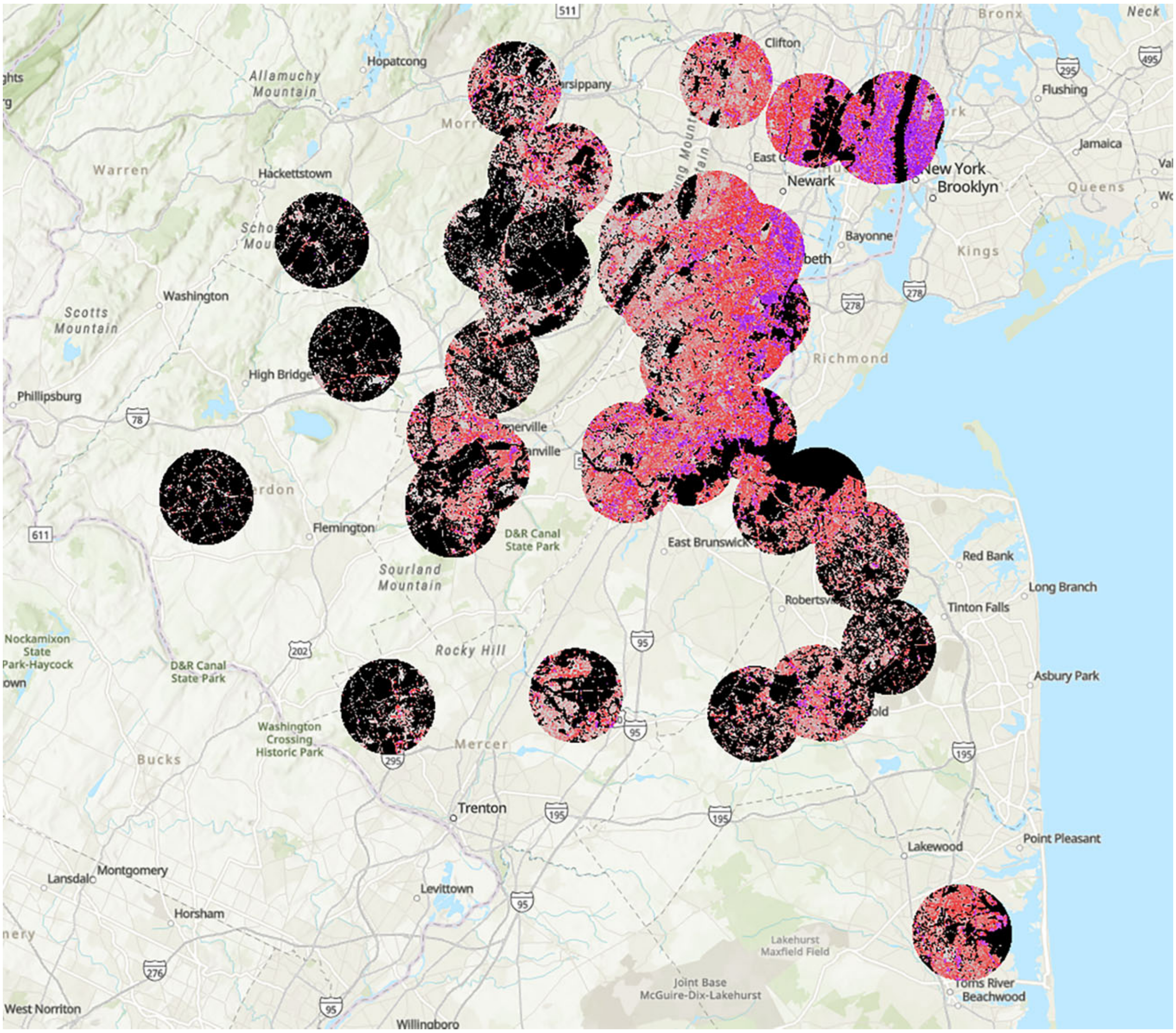

Fig. 1 We sampled 2405 adult spotted lanternflies (*L. delicatula*) from 93 locations in New Jersey, USA, in 2021. For each sample site, we calculated the mean percent impervious surface within a 5-km buffer. Circles show the buffer zone and impervious surface within it for each site, with little impervious surface represented by black and the most impervious surface represented by purple.

impervious surface for the study site buffer zones ranged from 1.9% to 65.0%. Given elevation can also affect environmental temperatures, with corresponding potential to affect ectotherm body size (e.g., Brehm et al. 2019), we used ArcGIS to quantify the elevation of each sample site.

Statistical analyses

We conducted all statistical analyses in R v. 4.3.2 (R Core Team 2023). We fit linear mixed effects models with the *lmer* function of *lme4* (Bates et al. 2015) to test for a relationship between mean percent impervious surface and spotted lanternfly body length. We ran models separately for males and females to account for sex-specific differences in body length (Fig. 2) and differential effects of the model variables. Models included mean percent impervious surface and latitude as fixed effects and sample site as a random effect to account for the non-independence of samples collected from the same location. Latitude was included as a covariate to model the effects of this variable on environmental temperature and other latitude-related environmental conditions (e.g., day length) that could affect body length. Both models also included the quadratic terms for percent impervious surface and latitude to model curvilinear relationships between these variables and body length that were apparent during preliminary data visualization and evaluation of regression diagnostics. We did not include altitude in the models

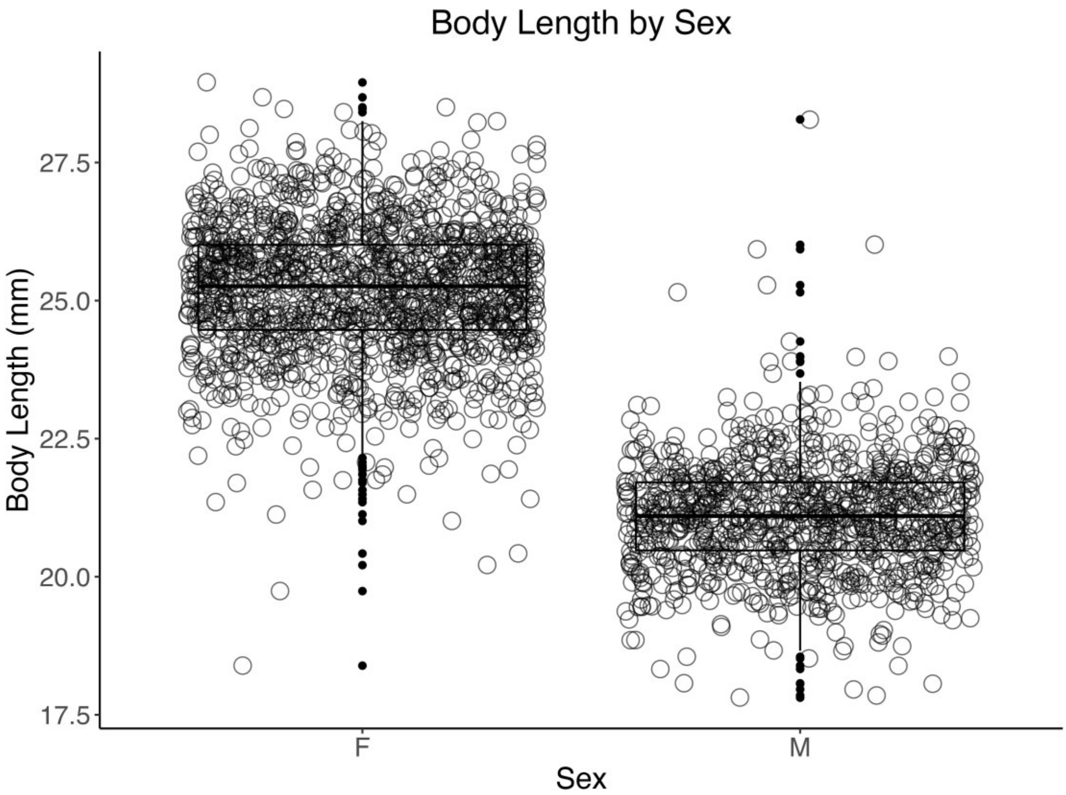

Fig. 2 Female spotted lanternflies (*L. delicatula*) had significantly larger mean body lengths (25.194 mm + 1.232 mm) than males (21.103 mm + 1.034 mm; Welch two-sample *t*-test: $t = 88.087$; $P < 0.001$).

because we found a significant and substantial negative correlation between altitude and percent impervious surface in both the male and female data sets (male Pearson's correlation = −0.733; $t = -33.65$; $P < 0.001$; female Pearson's correlation = −0.688; $t = -35.679$; $P < 0.001$).

Prior to fitting the models, we performed sex-specific scaling of mean percent impervious surface and latitude. We tested for multicollinearity of the fixed effects, including their quadratic terms, by calculating variance inflation factors (VIFs) using the *car* package (Fox and Weisberg 2019). All VIFs for fixed effects in the models (including quadratic terms, which have inherent multicollinearity) were <3, indicating low and acceptable multicollinearity among the variables. We also assessed multicollinearity for models without the quadratic terms for latitude and mean percent impervious surface and confirmed that there was low multicollinearity between latitude and mean percent impervious surface (= ∼ 1). After running the global models, we performed model selection by comparing the AIC of models of varying degrees of complexity using the *dredge* function of *MuMIN* (Barton 2024). We performed model averaging of those top models with $\Delta\text{AIC} < 2$ and evaluated the *P*-values of the full model-averaged coefficients for significance. We then used *Dharma* (Hartig 2017) to evaluate the model residuals. We also calculated the mean body length of males and females collected from the most (≥50% mean impervious surface) and least (≤15% mean impervious surface) urbanized areas and statistically compared them via Welch's two-sample *t*-tests.

Heat tolerance experiment

From July 22 to July 31, 2024, we collected 70 adult female and 60 adult male spotted lanternflies from the base of the STEM building at Kean University (Union, NJ). All adults were collected from the same urbanized area (∼61% mean impervious surface) to avoid confounding effects of potential local adaptation and/or phenotypic plasticity on thermal response. Adults had eclosed approximately 1 week prior and were therefore unlikely to have traveled far from their developmental habitat (e.g., Keller et al. 2020). Females were not yet gravid given the time of year that we sampled. We collected adults by hand and placed them in an empty glass aquarium in a lab within the STEM building, where they acclimated to room temperature (∼20°C) for approximately 30 min.

We filled a water bath (2-liter VWR® General Purpose Water Bath; cat. 76308-830) with distilled water

Table 1. We fit sex-specific linear mixed models to test the effects of mean percent impervious surface and latitude on spotted lanternfly (*L. delicatula*) body size.

	Males			Females		
Fixed effect	**Estimate**	**SE**	***P***	**Estimate**	**SE**	***P***
% Impervious surface	0.125	0.049	**0.011**	0.253	0.054	**<0.001**
% Impervious surface^2	– 0.027	0.052	0.596	0.053	0.076	0.482
Latitude	0.202	0.073	**0.006**	0.065	0.077	0.4
Latitude^2	0.124	0.038	**0.001**	0.138	0.039	**<0.001**

Linear models included quadratic terms for mean percent impervious surface and latitude to model non-linear relationships between these variables. Models also included site as a random effect. Prior to running the models, we scaled the predictor variables. Model-averaged coefficients for models with ΔAIC < 2 are presented. Bold text indicates significance ($p < 0.05$).

and heated it to 50°C. The water temperature was held constant at 50°C, with the temperature monitored via an RTD probe (VWR® Traceable Temperature Data Logger; cat. 76321–892) suspended in the center of the water bath. We placed individual lanternflies into room-temperature plastic 50-ml conical vials with the lids closed, such that the individual was able to stand and walk around the conical vial and the vial was watertight. We then immediately used test-tube tongs to submerge each vial horizontally into the center of the water bath. We started a timer at the moment that the conical vial was submerged into the water bath and stopped the timer at the moment that the individual exhibited signs of having reached its critical thermal maximum (i.e., CT_{max}, indicated by muscle spasms and loss of coordinated movements; Lutterschmidt and Hutchison 1997; Orsted et al. 2022). At this point, we removed the individual from the vial, used digital calipers to measure its body length as above, and weighed it using a microbalance (Mettler Toledo New Classic MS; cat. MS303S). We then immediately preserved the majority of individuals in 100% ethanol for future analyses. However, we temporarily placed several random individuals in empty plastic pipette tip boxes to allow them to regain coordinated muscle function to confirm that these physical symptoms indicated the moment at which the CT_{max}, rather than the lethal thermal limit, was reached.

We removed four data points for females and one data point for males from analyses due to data collection issues during these five heat tolerance trials, resulting in 66 and 59 heat tolerance trial results retained for females and males, respectively. We used linear regressions to model the relationship between spotted lanternfly body length and time to reach CT_{max}. We fit regression models using the *lm* function in the package *lmtest* (Zeileis and Hothorn 2002). We fit linear models separately for males and females to account for sex-specific size differences as well as potential sex-specific responses to environmental temperature. We also used sex-specific linear regressions to test for a relationship between spotted lanternfly weight and time to reach CT_{max}. We checked the model assumptions via residual diagnostics plots and a Shapiro-Wilk test for normality.

Results

Effects of urbanization on spotted lanternfly body length

Female spotted lanternflies were significantly longer than males (females = 25.194 mm ± 1.232 mm; males = 21.103 mm ± 1.034 mm; Welch two-sample *t*-test: $t = 88.087$; $P < 0.001$; Fig. 2). A statistically significant effect of mean percent impervious surface on body length was present for both females and males (Table 1). The mean body lengths for females and males in areas with the most urbanization (≥50% mean impervious surface) were 25.504 mm (±1.103 mm) and 21.148 mm (±1.069 mm), respectively, whereas the mean body lengths for females and males in areas with the least urbanization (≤15% mean impervious surface) were 24.868 mm (±1.233 mm) and 20.673 mm (±1.043 mm), respectively. Mean body lengths differed significantly among the most and least urbanized environments (female *t*-test: $t = 7.776$; $P < 0.001$; male *t*-test: $t = 4.207$; $P < 0.001$). Both males and females also displayed a non-linear effect of latitude on body size, with a significant positive linear effect of latitude on body size present for males as well (Table 1).

While most residual diagnostic tests were not significant, *Dharma* did identify five statistical outliers for males and three for females. We re-ran the linear mixed models without these outliers to assess their effects, and we found no changes to the significance of the fixed effects in either model.

Effects of spotted lanternfly body size on heat tolerance

Females in the trials were significantly longer (females = 25.8 mm ± 1.2 mm; males = 21.2 mm ± 1.1 mm; Welch's two-sample *t*-test: $t = 22.8$, $P < 0.001$)

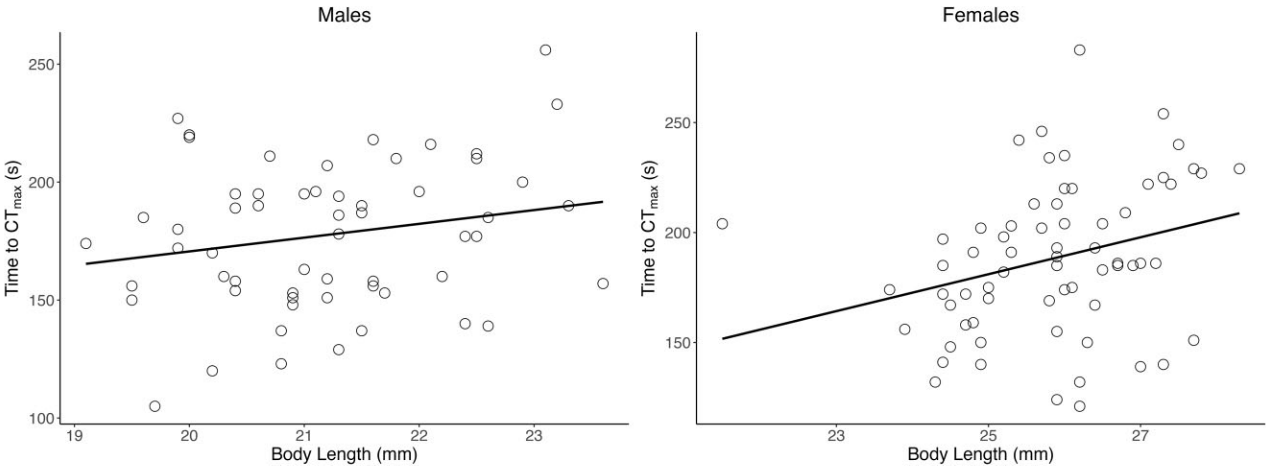

Fig. 3 We fit sex-specific regression models to test for an effect of body length on time to reach critical thermal maximum ($\mathrm{CT}_{\mathrm{max}}$) in spotted lanternflies (*L. delicatula*). We found a significant effect of body length on time to reach $\mathrm{CT}_{\mathrm{max}}$ for females ($P = 0.018$) but not males ($P = 0.126$).

and heavier (females = 0.2 g ± 0.05 g; males = 0.12 g ± 0.03 g; Welch's two-sample t-test: $t = 9.9$, $P < 0.001$) than males, consistent with our observations from our urbanization study. We found a significant effect of body length on time to reach $\mathrm{CT}_{\mathrm{max}}$ for females (estimate = 8.394; SE = 3.462; $P = 0.018$) but not males (estimate = 5.843; SE = 3.759; $P = 0.126$; Fig. 3). Importantly, we did not find a significant effect of weight on time to reach $\mathrm{CT}_{\mathrm{max}}$ for females (estimate = 137.89, SE = 77.75, $P = 0.081$) or males (estimate = 169.97, SE = 142.93, $P = 0.239$). Of note, we noticed a movement in spotted lanternflies that was indicative of individuals having reached their $\mathrm{CT}_{\mathrm{max}}$; just before the loss of coordinated movement, spotted lanternflies consistently spread their wings.

Discussion

Is larger body size in more urbanized areas the result of plasticity in developmental rate?

The temperature-size rule states that developmental rate is plastic and related to environmental temperature in ectotherms, such that warmer temperatures are expected to result in faster development and smaller adult body size (Atkinson 1994; Angiletta and Dunham 2003). Indeed, developmental rate in spotted lanternflies correlates positively with environmental temperatures up to 30°C (Kreitman et al. 2021), and egg masses collected from environments with warmer mean temperatures hatch earlier (Keena et al. 2023). The relationship between developmental temperature and body size in spotted lanternflies is somewhat more tenuous. Spotted lanternfly nymphs raised under temperature regimes that included periods of exposure to hot temperatures (i.e., 35°C–40°C) were found to have lower newly molted weights than those raised under constant lower temperatures (Keena et al. 2023), demonstrating a negative correlation between hotter environmental temperatures and a metric of spotted lanternfly body size, whereas rearing temperatures of 20°C, 25°C, and 30°C were found to have no effect on adult wing length (Kreitman et al. 2021; i.e., a metric similar to the body length metric used herein). One would thus predict that urban environments would promote faster development and corresponding smaller adult body size or have no effect on body size (e.g., Kreitman et al. 2021). However, we found that both adult males and females were significantly larger in more urbanized areas. We therefore find it unlikely that plasticity in developmental rate in response to the urban heat island effect is responsible for the larger body size observed in spotted lanternflies in this study.

An alternative explanation for our observations is that urban heat islands extend the time available for development in Northern latitudes, which would otherwise be truncated by the colder climate. However, our results suggest that this is unlikely. We included latitude as a covariate in our statistical models, and we found a positive effect of latitude on body size for males and no effect for females (Table 1). If this alternative hypothesis were supported, we would expect to see a negative effect of latitude on body size. As this species primarily inhabits more Northern latitudes in the United States, testing of this hypothesis is not currently possible, but it should be explored if the range of this species expands to cities in the Southern United States.

We considered the possibility that larger spotted lanternfly body size in cities is due to differences in diet in urban areas, as nutrition can affect insect growth and developmental rate (Chown and Gaston 2010; Koyama and Mirth 2018). The tree-of-heaven (i.e., the preferred host of the spotted lanternfly) is more abundant in cities (Cook et al. 2021), and nymphs raised with access to tree-of-heaven develop more quickly (Uyi et al. 2020, 2021). Yet, recent work has shown that species of host plant, including tree-of-heaven, has no effect on adult forewing length (Kreitman et al. 2021), a metric similar to the metric of body length used herein. Given this lack of relationship, we also find it unlikely that diet differences related to urbanization are responsible for the larger body sizes observed in more urbanized areas.

Lastly, we considered whether elevation could be responsible for the larger body sizes observed in urbanized areas. Elevation could not be included in our linear mixed models due to high multicollinearity with mean percent impervious surface, but one would expect that elevation would correlate positively with spotted lanternfly body size since higher elevations have lower environmental temperatures (e.g., Brehm et al. 2019). However, males showed no correlation between elevation and body length (Pearson's correlation coefficient = 0.012; $t = 0.362$; $P = 0.713$), whereas females displayed a significant negative correlation (Pearson's correlation coefficient = −0.132; $t = -5.016$; $P < 0.001$), a pattern in contrast to that expected based on the temperature-size rule and which is most likely a result of the high correlation between urbanization and elevation.

Could larger body size be advantageous for urban spotted lanternflies?

In this study, we did not test whether larger body size is adaptive for spotted lanternflies in cities. Nonetheless, we consider here several advantages of larger body size in cities that may have the potential to promote adaptive evolution in spotted lanternflies. First, there may be thermal advantages to larger body sizes for urban spotted lanternflies. Larger ectotherms have smaller surface-area-to-volume ratios, resulting in greater thermal inertia (Bartholomew and Heinrich 1978), which may protect against short-term exposure to temperature extremes (Shepherd et al. 2008). Indeed, spotted lanternflies in urban areas may have frequent short-term encounters with high temperatures when landing on asphalt or the sides of metal buildings (e.g., Frank and Cowper 2022). Surface-area-to-volume ratio may also affect the rate of evaporative water loss, with larger ectotherms better protected against water loss when exposed to high temperatures in urban areas (Kühsel et al. 2016). Several species of insects have shown larger individuals to have higher thermal tolerance (e.g., army ants, Baudier and O'Donnell 2018; red imported fire ant, Wendt and Verble-Pearson 2016; fruit flies, Leiva et al. 2024; tsetse flies, Weaving et al. 2023) and smaller individuals to have greater rates of evaporative water loss (e.g., Diptera, Hymenoptera, Coleoptera, and Lepidoptera spp.; Kühsel et al. 2016).

In this sense, the larger body sizes observed in urban spotted lanternflies in our study could be advantageous for living in cities. Our heat tolerance trials yielded some support for this hypothesis. We found that the time required to reach CT_{max} was significantly related to female body length, with a similar (though non-significant) trend evident for males. The lack of a significant effect of body length on time to CT_{max} in males may stem from the difference in body length among males and females and its corresponding effect on surface-area-to-volume ratio. Surface area and volume scale allometrically, such that the smaller size of males may correspond to a dramatically higher surface-area-to-volume ratio for males than females, which reduces thermal inertia and its buffering effect against hot temperatures. Importantly, the difference in significance between male and female responses to temperature is not due to sex-based differences in weight. Although females are often heavier than males (Wolfin et al. 2019), we found no effect of weight on time to CT_{max} for either sex. In other words, body length, but not weight, predicts resistance to hot temperatures in spotted lanternflies.

Larger body size in cities may confer other benefits as well. Cities have highly fragmented habitats compared to non-urban areas, such that individuals may have to travel among distant habitat patches. Thus, larger body size may increase the dispersal capacity of individuals in cities (Merckx et al. 2018). To the best of our knowledge, the relationship between body length as measured herein and dispersal distance has not yet been studied in spotted lanternflies (but see Wolfin et al. 2019 for a study of other morphological traits that affect flight capacity). However, insects for which there is a relationship between size and dispersal distance are larger in cities (Merckx et al. 2018), and larger body size in some urban insects has been attributed to habitat fragmentation (e.g., bumblebees; Theodorou et al. 2021). Importantly, selection for larger body size for reasons other than thermal tolerance (e.g., for dispersal capacity) can have the secondary benefit of buffering spotted lanternflies against short-term temperature extremes (Brans et al. 2017), potentially increasing the strength of directional selection on body size in urban populations.

Conclusion

We found that invasive spotted lanternflies from more urban areas had significantly longer body lengths and that body length was positively correlated with resistance to hot temperatures for females. While we cannot conclusively exclude plasticity in developmental rate as an explanation for these observations, the totality of our results suggests advantages of larger spotted lanternfly body size in cities, which may be supportive of an adaptive explanation. The results of our study thus suggest that urban areas may play an important role in the ecology and, potentially, evolution of this invasive species.

Author contributions

B.A.L. conceived of the study and acquired the funding. A.M. and R.M. measured samples and curated the data set. R.M. conducted all GIS work. B.A.L. conducted all statistical analyses. B.A.L. and A.M. designed the heat tolerance trials, and A.M. oversaw the work of the Group Summer Scholars Research Program participants. B.A.L. wrote the first draft of the manuscript. All authors contributed to editing the manuscript.

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Data availability

The data sets and R code used for analyses are available on GitHub (https://github.com/brenna-levine/SLF_Body_Size).

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