

ABSTRACT

Title of Thesis: THE INFLUENCE OF THERMAL ENVIRONMENT ON DEVELOPMENT AND VULNERABILITY TO PREDATION OF THE AZALEA LACE BUG, *STEPHANITIS PYRIOIDES* (HETEROPTERA: TINGIDAE)

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Differential thermal environments were examined for their influence on performance traits of a key ornamental pest, the azalea lace bug, *Stephanitis pyrioides*, in the presence and absence of a generalist predator, the green lacewing, *Chrysoperla carnea*.

In laboratory studies, duration of development increased for nymphal instars of *S. pyrioides* as temperature decreased, producing significant developmental lags in cooler environments. Predation trials identified early nymphal stages as more susceptible to predation than older, dispersal-capable stages, specifically in warmer environments. Additionally, morphological characteristics attained at adulthood combined with behavioral defenses may mediate the reduction in consumption of later *S. pyrioides* stages by piercing-sucking arthropods such as *C. carnea*.

Field studies confirmed development and life-stage vulnerability findings from the laboratory, however, differential thermal environments created by shading did not generally influence predation. In urban landscapes, *S. pyrioides* may attain a degree of enemy-free space by occupying a thermal refuge in sunny, exposed habitats.

THE INFLUENCE OF THERMAL ENVIRONMENT ON DEVELOPMENT AND
VULNERABILITY TO PREDATION OF THE AZALEA LACE BUG,
STEPHANITIS PYRIOIDES

by

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DEDICATION

I dedicate this thesis to my loving and supportive family. To my mother, Karen, for nurturing creativity in all endeavors and giving perspective to the natural world, to my father, Ronald, for instilling a sense of logic and appreciation for careful thought, and to my sister, Erica, for encouraging adventure and purpose. To my parents-in-law, Ratnakumari (Atthamma) and Narayana Battula, for welcoming me into their home as if I was their natural son. Finally, I dedicate this thesis especially to my darling wife, Kavita, who has nourished me with great culinary delights and patiently awaited the completion of this work.

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Chapter I

Stephanitis pyrioides development and vulnerability to predation by *Chrysoperla carnea* at three temperatures

ABSTRACT

Three thermal regimes (18, 21, and 24°C) were tested to determine their influence on the development of a specialist insect pest, the azalea lace bug, *Stephanitis pyrioides* (Scott) (Heteroptera: Tingidae), as well as *S. pyrioides* survival and dispersal in the presence and absence of a generalist predator, the green lacewing, *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae).

Duration of development increased for nymphal instars of *S. pyrioides* as temperature decreased, producing significant developmental lags for the second, third, and fifth stadia, relative to *S. pyrioides* in higher temperature environments. Each 3°C differential between temperature treatments translated into an approximate 7 d differential in nymphal developmental for *S. pyrioides*. In 36 h predation trials using saturated prey densities for nymphal and adult stages of *S. pyrioides*, a significant temperature by life-stage interaction revealed that early instars were consumed more than later instars or adults as temperature increased. Predation of second instar *S. pyrioides* by second instar *Chrysoperla carnea* was 2 times greater than later nymphal instars, and 7 times greater than adults. Later nymphal stages were consumed 3 times more than adults, who were rarely consumed by predators. Reduced predator-inflicted mortality for later stages was partially explained by higher dispersal. In addition, morphological characteristics attained at adulthood combined with behavioral defenses may mediate the

reduction in consumption of later *S. pyrioides* stages by piercing-sucking arthropods such as *Chrysoperla carnea*.

Predation trials identified early nymphal stages as more susceptible to predation than older, dispersal-capable stages, specifically in warmer environments. These studies suggest that *S. pyrioides* vulnerability to predation in natural systems may be highest for immature stages in sunny, warmer habitats, and lowest for adults in shady, cooler habitats. The influence of thermal environment on life-stage duration as it applies to life-stage vulnerability is discussed in the context of natural enemy mediated herbivore regulation and pest management.

INTRODUCTION

Environmental temperatures govern body temperatures for terrestrial ectothermic organisms (Chapman 1998) and may dictate their exploitation of resources in space and time (Tracy and Christian 1986). For ectothermic insects, thermal habitat variation may influence several activities, including aggregation, foraging, and dispersion (Barrett and Chiang 1966, Kramm and Kramm 1972, Shreeve 1986, Shultz and Hadley 1987, Carruthers et al. 1992, Shultz 1998). Temperature may also influence insect herbivore development (Neal and Douglass 1988, Stamp and Bowers 1990, Braman et al. 1992, Braman and Pendley 1993, Shrewsbury 1996, Milonas and Savopoulou-Soultani 2000, Sipura and Tahvanainen 2000) and the period of time life-stages may be vulnerable to predation (Shrewsbury 1996, Lepping and Shrewsbury unpubl.). Although some insect predators (Pearson and Lederhouse 1987, Schultz 1998) and herbivores (Carruthers et al. 1992, Frid and Myers 2002) thermoregulate through sun-basking behaviors

(heliothermy), many insect predators and their prey may be subject to ambient thermal conditions (poikilothermy), especially when mobility is limited.

As environmental temperature increases, metabolic rates increase for ectothermic predators, creating demand for higher rates of prey consumption (Ba M'Hamed and Chemseddine 2001). For generalist predators, developmental rates (Alauzet et al. 1994, Wright and Chambers 1994, Parajulee et al. 1995, Stamp et al. 1997, Ba M'Hamed and Chemseddine 2001, Islam and Chapman 2001, Perdikis and Lykouressis 2002) and prey consumption (Crocker et al. 1975, Grafius and Warner 1989, Giroux et al. 1995, Anderson et al. 2001, Islam and Chapman 2001) generally increase as temperature increases.

Common green lacewings, *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae) are generalist predators that have been studied in detail as biological control agents (Canard et al. 1984, McEwen et al. 2001). In accord with other lacewing species (Islam and Chapman 2001), *Chrysoperla carnea* prey consumption has been found to increase as temperature increases (Sundby 1966, Scopes 1969, El-Wakeil 2003). While lacewing predation rates under varying temperatures have been examined for some agricultural pests (Sundby 1966, Scopes 1969, El-Wakeil 2003), the influence of varying temperatures on *Chrysoperla carnea* predation of ornamental pests is virtually unknown.

In landscape habitats, *Chrysoperla carnea* have been found in association with a key ornamental pest, the azalea lace bug, *Stephanitis pyrioides* (Scott) (Heteroptera: Tingidae) (Trumbule 1989, Shrewsbury 1996, Stewart 2000). *Stephanitis pyrioides* damage azalea by extracting leaf mesophyll from the underside of leaves, resulting in a stippled appearance on the topside of leaves (Klingeman et al. 1999). Relatively small

levels of feeding damage ($\cong 1\%$) may result in rejection of nursery-grown azalea at the point-of-sale (Klingeman et al. 2000). *Stephanitis pyrioides* is a specialist of azalea, and completes five nymphal stages before eclosing to adult. Mated adults remain to feed and oviposit on host plants for relatively long periods (Bailey 1951, Lepping, personal observation.). The annual appearance of feeding stages of *S. pyrioides* begins in late April to early May in Maryland (MD), U.S., and multiple generations may occur throughout the year (Neal and Douglass 1988). Laboratory and field studies have described the effects of varying thermal environments on *S. pyrioides* development (Neal and Douglass 1988, Braman et al. 1992, Shrewsbury 1996). For example, Braman et al. (1992) examined *S. pyrioides* development at seven constant temperatures (15-33°C), and found *S. pyrioides* to successfully complete development at all temperatures except 33°C. Increasing temperature accelerated nymphal *S. pyrioides* development, although temperatures over 24°C resulted in deceleration of developmental rates (Braman et al. 1992). Similarly, Shrewsbury (1996) found accelerated *S. pyrioides* growth with increasing degree-day accumulations in urban landscape habitats.

Population levels of *S. pyrioides* have been observed to vary in urban landscape habitats. Of several components of vegetational texture examined, Shrewsbury and Raupp (2000) found structural complexity was the best predictor of patterns in *S. pyrioides* abundance. Shrewsbury and Raupp (2000) estimated the structural complexity of a habitat by measuring the occurrence of vegetation in distinct strata (e.g. ground/turf layer, annual/perennial layer, shrub layer, understory layer, overstory layer). Of the five vegetational strata measured at 24 landscape sites, 71% of the variation in *S. pyrioides* abundance predicted by structural complexity was explained by the presence or absence

of an overstory layer (Shrewsbury and Raupp 2000). Azalea in structurally simple habitats, which generally lacked understory or overstory layers, received greater periods of light exposure and subsequently higher temperatures. Conversely, azalea in structurally complex sites were found to receive less direct sunlight, which translated into lower temperatures in those habitats. Structurally complex sites supported fewer *S. pyrioides* (Shrewsbury and Raupp 2000), more natural enemies, and greater *S. pyrioides* mortality (Shrewsbury 1996). Although Shrewsbury (1996) found *S. pyrioides* developed slower in cooler, complex habitats, where generalist predators and *S. pyrioides* mortality were greater, the precise role that temperature plays in *S. pyrioides* – predator interactions is poorly understood.

The overall objective of this study was to elucidate the role that varying thermal environments play in herbivore – predator interactions. Previous studies have examined development of *Chrysoperla carnea* (Carnard et al. 1984) and *S. pyrioides* (Braman et al. 1992) in varying thermal environments. Additionally, predation by *Chrysoperla carnea* and other generalist predators has been examined on *S. pyrioides* at ambient temperatures (Shrewsbury 1996, Stewart et al. 2002). This study aims to describe the potential of a predator driven, thermal-mediated mechanism for explaining observed patterns of *S. pyrioides* abundance in urban landscape systems. To evaluate this mechanism, *S. pyrioides* development and vulnerability to predation by *Chrysoperla carnea* were examined in varying thermal environments. The specific objectives of this study were: (1) to determine the effect of varying thermal environments on *S. pyrioides* development, and (2) to determine the effect of varying thermal environments on *S. pyrioides* life-stage vulnerability to predation.

METHODS

TREATMENT TEMPERATURES

Selection of temperatures used in the laboratory was based on the thermal environments that early annual generation *S. pyrioides* are likely to experience in structurally simple and complex urban landscapes in Maryland, U.S. Temperature records for the month of May were used to set the lower treatment level, as the first annual occurrence of *S. pyrioides* nymphs in Maryland typically begins during early May (Neal and Douglass 1988). Mean monthly temperatures were derived from daily minimum and maximum temperatures selected for a nine-year period from local weather data (Maryland State Climatologist Office, College Park, MD). The mean temperature recorded under shaded conditions for Beltsville, MD, during May of the selected period is 18.0°C; the mean minimum and maximum temperatures (range) are 11.8, and 24.2°C, respectively. The 18.0°C value was assigned as the expected mean for a structural complex environment (full-shade) during the first annual generation of *S. pyrioides*.

Intervals between treatment temperatures were also selected to simulate temperature differentials between simple, exposed habitats, and complex habitats using the following procedure. Temperature measures were recorded in shaded northern and sunny southern exposure habitats, on either side of five, 3.2 m high walls oriented along an east – west transect, during August and September of 2001 at the Central Maryland Research and Education Center, Upper Marlboro, MD. Interplant temperatures were sampled at 12 min intervals and examined for differences between exposures using the MIXED procedure (SAS Institute 2003). The 2001 survey revealed a difference of 2.48°C between northern and southern exposures. Differential temperature measurements

for northern and southern exposure environments in the fall 2001 survey were used to approximate spring conditions, since spring and fall illumination periods are similar in terms of the orientation of the earth's axis of rotation to the sun (University of Oregon, Solar Radiation Monitoring Laboratory, Eugene, Oregon). A previous field study examining temperatures between simple and complex landscape habitats revealed a difference of $\cong 2.5^{\circ}\text{C}$ (Shrewsbury 1996). Based on this collective information, treatment level spacing was selected at 3.0°C intervals. The following constant treatment levels were used in incubation chamber (Model I-36LLVL, Percival Scientific Inc., Perry, Iowa) studies: 18.0, 21.0, and $24.0 \pm 0.5^{\circ}\text{C}$. A photoperiod of 14:10 (L:D) was selected based on sunrise-sunset schedules (U.S. Naval Observatory, Astronomical Applications Department), to approximate light exposure periods during May.

***STEPHANITIS PYRIOIDES* DEVELOPMENT AND SURVIVAL IN THE ABSENCE OF PREDATORS**

To examine lace bug developmental time at controlled temperatures, *S. pyrioides* were collected from a single field population in College Park, MD. Host-plants, 2 year-old azalea, *Rhododendron mucronatum* (Blume) G. Don (var. Delaware Valley White) (Ericaceae: Rhododendron), used in laboratory experiments were obtained from a commercial nursery and maintained under uniform growing conditions until treatment assignment. Two replicates were arranged as a randomized complete block design with 110 subsamples. A time block was required to control for incubation chamber effects. Newly emerged first or second instar lace bug nymphs were transferred individually to 3 cm long, terminal-end (new-growth) cuttings of azalea using a camel hair paintbrush (1 nymph/cutting). Cuttings were placed in 60 mm diameter by 15 mm depth petri dishes lined with moistened filter paper (55 mm diameter, no. 1), sealed in resealable plastic

bags to maintain humidity, and introduced into incubation chambers such that individuals were oriented in their natural, inverted positions (i.e. abaxial leaf surface down). Filter paper liners were remoistened, and water condensation was removed daily. Lace bugs were monitored daily until adult eclosion, to determine life stage and number surviving. Upon adult eclosion, individuals were identified to sex.

STATISTICAL ANALYSIS

Mean values for duration of nymphal development were estimated only using individuals completing each stadium, to reduce within stage or previous stage variation. Development and survival measures were compared using the MIXED procedure (SAS Institute 2003). Frequencies of sexes were tabulated using the FREQ procedure. To examine *S. pyrioides* instar-specific thermal developmental unit requirements, linear developmental models were constructed and degree-day calculations were performed (after Braman et al. 1992). Lower developmental threshold temperatures (T_o) were calculated by extrapolating the linear regression line to the x-axis of a graph with the reciprocal of developmental time on the y-axis, and increasing temperature on the x-axis. Mean thermal requirements (K) for each instar were determined using the mean of K_t , which was calculated with the following equation:

$$K_t = (T - T_o) * D_t,$$

where T was 18, 21, or 24°C; T_o was the temperature threshold for a specific instar; D_t was the mean developmental time (in days) for a specific instar at temperature T (after

Braman et al. 1992). Only the development times of *S. pyrioides* that completed instars two through five were used to estimate the lower developmental threshold (T_o).

***STEPHANITIS PYRIOIDES* SURVIVAL IN THE PRESENCE AND ABSENCE OF PREDATORS**

Laboratory studies were conducted to examine the influence of temperature on *S. pyrioides* survival in the presence and absence of predators. Survival experiments examined lace bug nymphal instars two through five, and the adult stage. The vulnerability of each life stage to predation was examined discretely to enable comparison of predator inflicted mortality and duration of development for each nymphal instar.

Twelve replicates were arranged as a randomized complete block, double split-plot design with a 3x5x2 factorial treatment structure (temperature:life-stage:predation). Whole-plots included the three treatment temperatures (18, 21, and 24°C) used in the development experiments; the primary sub-plot included life-stage (nymphal instars 2-5, and adults), and the secondary sub-plot included a predator treatment (predator absent or predator present).

Survival arenas were comprised of 150 mm diameter by 15 mm depth petri dishes lined with filter paper (125 mm, no. 1) and contained a 3 cm length cutting of new growth *R. mucronatum*, each with three leaves (each leaf $\cong 3$ cm²). Initial prey (lace bug) densities were set at 20 individuals for each cutting. Dead prey items and molting prey items were replaced at each sampling interval to maintain initial prey densities. This method assured predators were never prey limited. Cuttings were placed in petri dishes and sealed in resealable plastic bags, and introduced into incubation chambers such that

individuals were oriented in inverted positions (abaxial leaf surface down). Filter paper liners were remoistened, and water condensation was removed at each sampling interval.

Predation was provided by introducing a single, second-instar *Chrysoperla carnea* (Rincon Vitova Insectaries, Inc., Ventura, CA), into predator treatments. A predator density of one individual lacewing larvae per petri dish was selected in order to avoid potential intraguild interactions (Canard and Duelli 1984, Rosenheim and Wilhoit 1993, Rosenheim et al. 1993, 1995). To avoid thermal shock and reduce effects of previous thermal environments, both predator and prey specimens used in survival experiments were segregated and acclimated to temperature treatments for a minimum of 2 h prior to predator treatment application. Survival experiments began at the start of a 14:10 (L:D) light-cycle, and were continued for a 36 h period. Prey density was monitored via visual observations, at 3 h intervals for 12 h. Sampling was discontinued for a 12 h period that included a 10 h dark period, after which the 3 h sampling regime and prey replenishment was reinstated for a final 12 h period. In preliminary tests, second instar *Chrysoperla carnea* larvae did not consume more than 20 prey items (2nd or 5th instars, or adults) during the predominantly dark 12 h period, when following a lighted 12 h prey saturation period.

***STEPHANITIS PYRIOIDES* DISPERSAL IN THE PRESENCE AND ABSENCE OF PREDATORS**

The influence of temperature on prey dispersal in the presence and absence of predators was also examined for each life-stage in the study described above. At each 3 h sampling interval, surviving *S. pyrioides* were scored for two positions, on the host-plant cutting or on the petri dish surface. *Stephanitis pyrioides* scored for the petri dish surface were considered to have dispersed.

***CHRYSOPERLA CARNEA* BEHAVIOR**

To examine the influence of temperature on *Chrysoperla carnea* in the presence of prey, predator behavior was recorded for the four following categories: searching/foraging, attacking, feeding, and resting. At each 3 h sampling interval, a 10 s period was allotted for observing and categorizing *Chrysoperla carnea* behavior. Searching/foraging was defined as continuous locomotion; attacking was defined as active probing of a prey item or prey-seizing; feeding was defined as active insertion of mandibles into a prey item with no locomotion; and resting was defined as no locomotion or feeding.

***STEPHANITIS PYRIOIDES* DEFENSIVE MORPHOLOGY AND BEHAVIOR**

In order to examine potential factors influencing variation in adult *S. pyrioides* vulnerability to predation, photographs were taken to document interactions of *S. pyrioides* with second instar *Chrysoperla carnea* larvae. Photography was shot for adult herbivores in closed petri dishes (to discourage emmigration) in the absence of predators, to document typical postures (stance). Predators were then introduced into petri dishes and interactions of predator and prey were photographed. While adult tingid morphology (e.g. expanded pronotal hood and mesonotal wing-pair), have been previously described (Drake and Ruhoff 1965) the defense characteristics and behavior of adult *S. pyrioides* have not been previously reported.

STATISTICAL ANALYSIS

Prey dispersal means were calculated as the proportion of surviving individuals off the host-plant cutting (petri-dish surface) during each 3 h sampling interval. For all *S. pyrioides* survival and dispersal data, repeated measures design with compound

symmetry covariate structure was used to analyze the following: (1) each instar or life-stage 3x2 factorial (temperature:predation) for prey mortality and prey dispersal, and (2) the 5x2 factorial (life-stage:predation) for accumulated mortality and prey dispersal. The 3x5x2 (temperature:life-stage:predation) factorial for prey mortality accumulated at each time point was compared using the MIXED procedure. All ANOVA procedures included the Kenward – Roger method for calculation of degrees of freedom, and maximum experimentwise error rates were limited with Bonferroni tests for all multiple mean comparisons. Frequencies for predator behaviors were tabulated using the FREQ procedure and compared using the chi-square or Fisher's exact test where appropriate (SAS Institute 2003).

RESULTS

***STEPHANITIS PYRIOIDES* DEVELOPMENT AND SURVIVAL IN THE ABSENCE OF PREDATORS**

Approximately one-half of initial sub-samples were first instar *S. pyrioides* nymphs, all remaining sub-samples began as second instar nymphs (Table 1). Successful development occurred at each of the three treatment temperatures. Mortality reached no more than 27% for any temperature level across all instars. The female/male sex ratio across all temperatures was 3:2.

Duration of nymphal development from the beginning of the second stadium through adult eclosion ranged from 13.3 d at 24°C to 26.6 d at 18°C. Temperature significantly affected *S. pyrioides* nymphal developmental time for all instars, except the fourth instar ($F = 10.31$; $df = 2, 2$; $P = 0.0884$) (Table 1). Developmental time was significantly longer at 18°C than 21 or 24°C for the second ($F = 64.97$; $df = 2, 2$; $P =$

0.0152), third ($F = 244.85$; $df = 2, 2$; $P = 0.0041$), and fifth ($F = 53.07$; $df = 2, 2$; $P = 0.0185$) instars, as well as for the sub-total of nymphal stages ($F = 49.48$; $df = 2, 2$; $P = 0.0198$). In addition, third instars developed significantly slower at 21 than 24°C (Table 1).

Construction of linear developmental models for *S. pyrioides* nymphal stadia allowed for estimation of instar-specific lower developmental temperature thresholds and associated degree-day requirements (Table 2).

Table 1. Mean \pm SE duration of development in days, and number of individuals completing each nymphal stage of *S. pyrioides* on 'Delaware Valley White' azalea cuttings at three temperatures

Temperature (°C)	Instar ^a				Sub-Total Nymphal ^b
	2	3	4	5	
18	5.5 \pm 0.2a (55)	5.9 \pm 0.1a (86)	5.9 \pm 0.4a (84)	9.6 \pm 0.4a (83)	26.6 \pm 1.0a (51)
21	3.7 \pm 0.2b (53)	3.6 \pm 0.1b (85)	4.3 \pm 0.4a (84)	6.6 \pm 0.4b (84)	18.1 \pm 1.0b (52)
24	2.7 \pm 0.2b (53)	2.7 \pm 0.1c (85)	3.3 \pm 0.4a (85)	4.7 \pm 0.4b (85)	13.3 \pm 1.0b (52)

Means followed by the same letter within a column are not significantly different ($P > 0.05$).

^a Values in parentheses are numbers of individuals completing each stage.

^b Values in parentheses are numbers of individuals completing stages 2 through 5.

Table 2. Linear thermal unit models, lower threshold temperatures (T_o) and mean thermal unit requirement (K) for development of each nymphal instar of *S. pyrioides*

Instar	Equation and adj.-r ² ^a	T_o , °C	K, DD ^b
Second	$Y = 0.0364t - 0.4712$ adj.-r ² = 0.4823	13.3	27.7
Third	$Y = 0.0371t - 0.5224$ adj.-r ² = 0.5224	14.1	24.9
Fourth	$Y = 0.0230t - 0.2366$ adj.-r ² = 0.3941	10.3	45.6
Fifth	$Y = 0.0196t - 0.2499$ adj.-r ² = 0.6301	12.9	51.9
Sub-total nymphal	$Y = 0.0064t - 0.0780$ adj.-r ² = 0.8591	12.2	156.8

^a Y , reciprocal of mean developmental times; t , temperature; adj.-r², adjusted coefficient of correlation.

^b Degree Days (DD) required to complete instar or sub-total of all nymphal instars.

STEPHANITIS PYRIOIDES SURVIVAL IN THE PRESENCE AND ABSENCE OF PREDATORS

Stephanitis pyrioides mortality in predator absent treatments was negligible for all nymphal and adult stages. Main effects of the predator treatment were significant for the second ($F = 202.31$; $df = 1, 561$; $P < 0.0001$), third ($F = 161.55$; $df = 1, 561$; $P < 0.0001$) fourth ($F = 161.44$; $df = 1, 561$; $P < 0.0001$), and fifth ($F = 209.62$; $df = 1, 561$; $P < 0.0001$) instars. Treatments with a predator present incurred higher mortality (Figure 1).

Examining discrete life stages, temperature by predation interactions occurred for second instars ($F = 8.08$; $df = 2, 561$; $P = 0.0003$), fifth instars ($F = 3.20$; $df = 2, 561$; $P = 0.0415$), adults ($F = 5.85$; $df = 2, 561$; $P = 0.0031$), and all stages pooled ($F = 12.11$; $df = 1, 561$; $P < 0.0001$). Life stages with significant temperature by predation interactions incurred slightly higher mortality as temperature increased from 18°C to 21/24°C (Figure 1a,d-f). However, no differences in mortality for this interaction were found between the 21 and 24°C levels for predator treatments for any *S. pyrioides* instar or the adult stage (Figure 1a-e).

Given negligible mortality in the predator absent trials, the effects of temperature, life stage and their interaction were examined for predator present treatments only. A significant temperature by life stage interaction ($F = 2.86$; $df = 8, 1,452$; $P = 0.0037$) identified higher mortality at higher temperatures for earlier life stages (Figure 2).

Across temperatures, predation by time interactions occurred for the second ($F = 2.87$; $df = 8, 561$; $P = 0.0039$), and fifth ($F = 6.20$; $df = 2, 561$; $P < 0.0001$) instars, as well as adults ($F = 4.76$; $df = 2, 561$; $P < 0.0001$). In addition, life-stage by predation interactions were significantly different across nymphal and adult stages ($F = 1.80$; $df = 32, 3,095$; $P < 0.0040$). The number of prey killed during each time interval decreased

over time for second and fifth instars, and increased for adults (Figure 3). The rate of prey consumption did not change over time for third or fourth instars. Predator-inflicted mortality was highest for second instars, and lowest for adults (Figure 3).

In general, the total number of *S. pyrioides* consumed by predators increased with time (Figure 4). Total predation at 36 h of second instar *S. pyrioides* by second instar *Chrysoperla carnea* was 2 times greater than predation of the third, fourth, and fifth *S. pyrioides* instars, for which there were no significant between-instar differences for total predation. Total predation of second instar *S. pyrioides* was 7 times greater than that of adults. The later nymphal instar “class” (3rd-5th instar *S. pyrioides*) were consumed approximately 3 times more than adults, who were rarely consumed during the 36 h period (Figure 4).

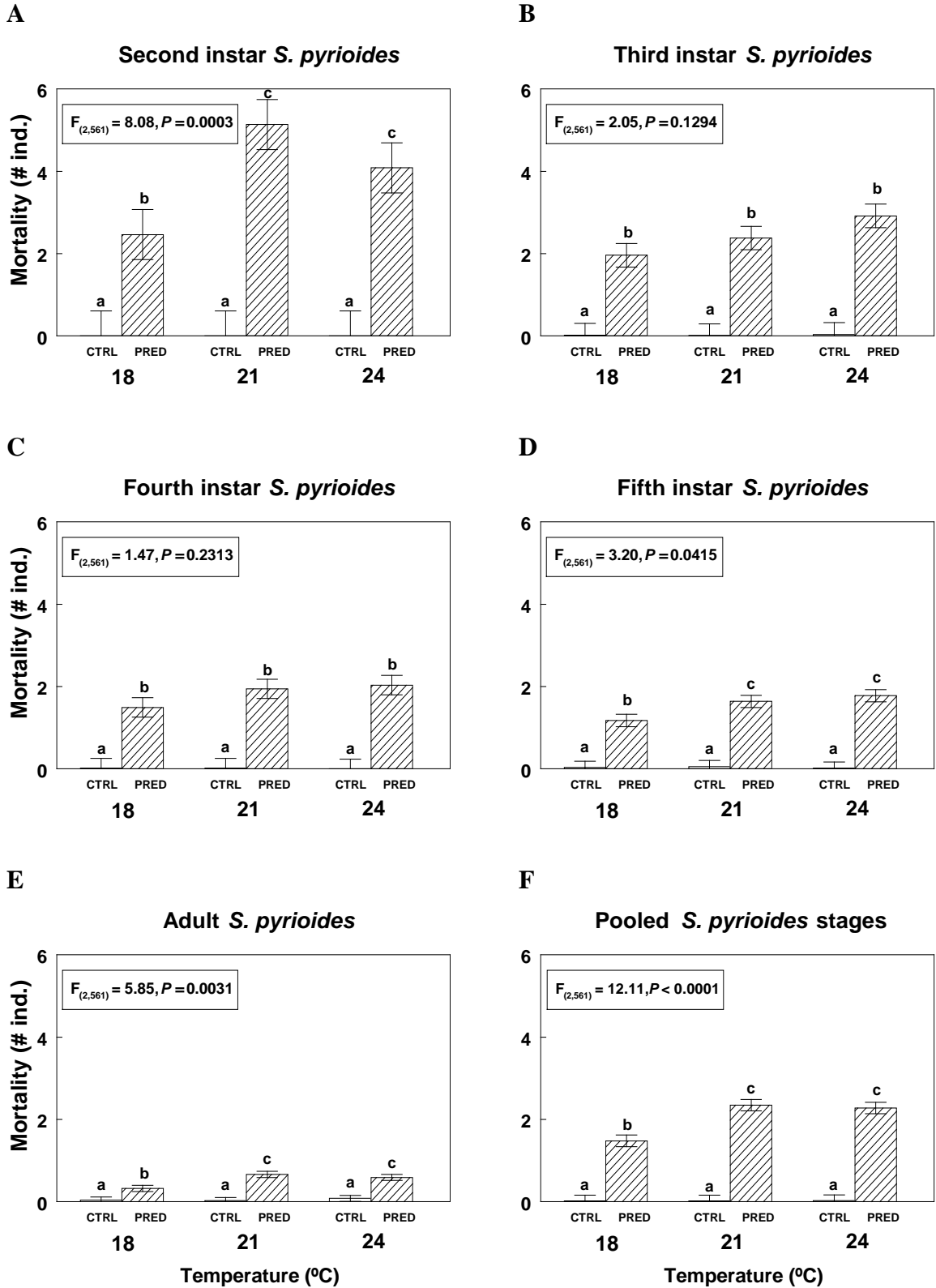


Figure 1. *Stephanitis pyrioides* life-stage mortality at three temperatures in predator absent (CTRL) and predator present (PRED) treatments (A-F). Means with the same letter are not significantly different (Bonferroni, $P > 0.05$).

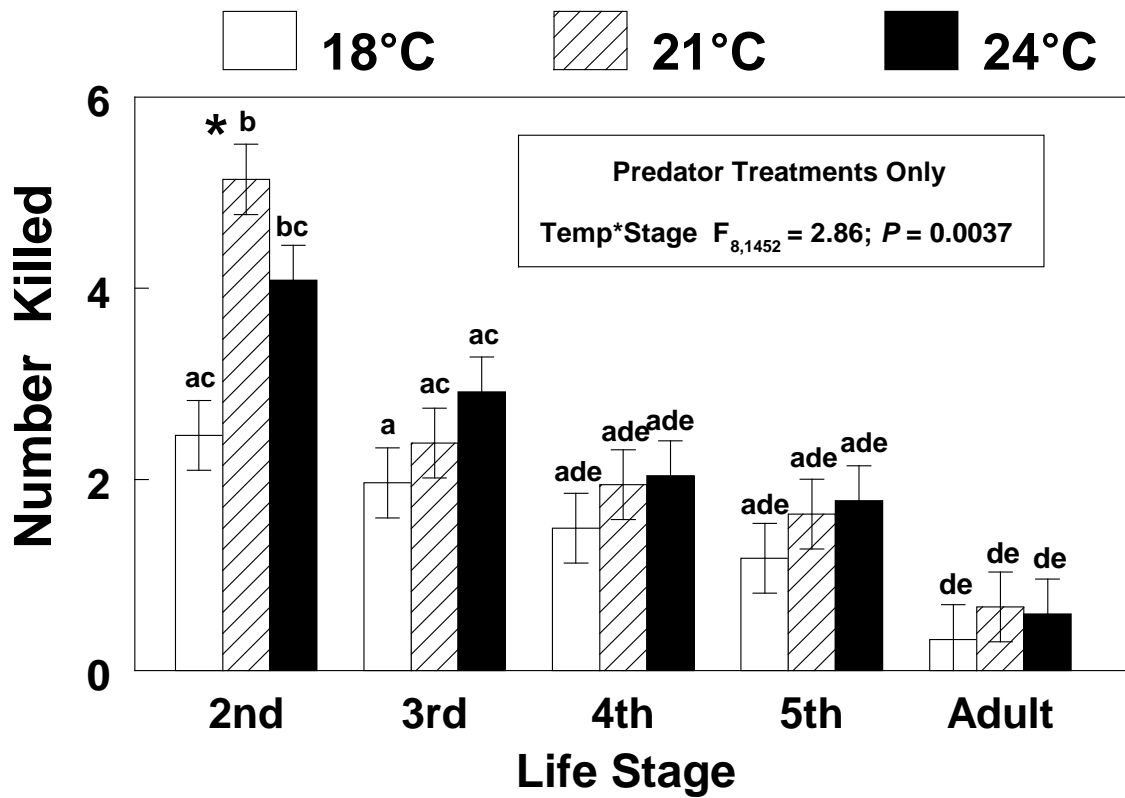


Figure 2. Mean \pm SE *Stephanitis pyrioides* killed over 36 h prey – saturation trials for nymphal and adult stages at three temperatures in the presence of a predator. Means with the same letter are not significantly different (Bonferroni, $P > 0.05$). Values with asterisks (*) denote significant temperature (Temp) by life-stage (Stage) interactions.

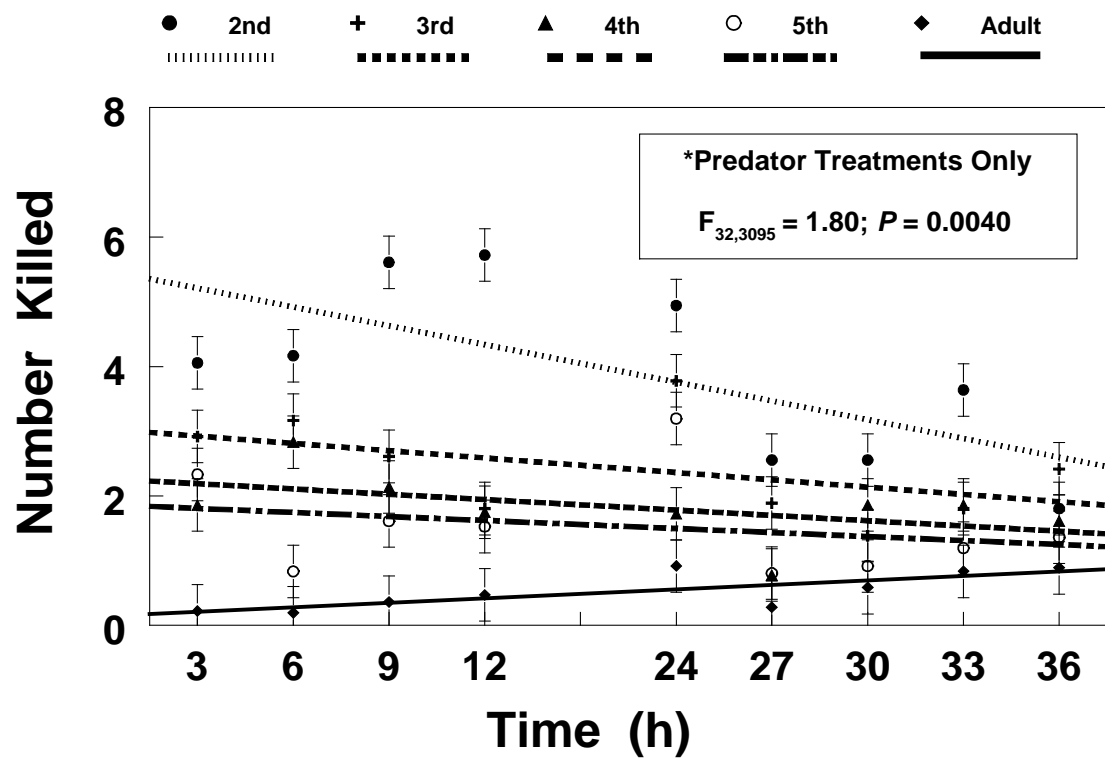


Figure 3. Number of *Stephanitis pyrioides* killed during each interval over 36 h prey – saturation trials, pooled across temperatures, for nymphal and adult stages in the presence of a predator.

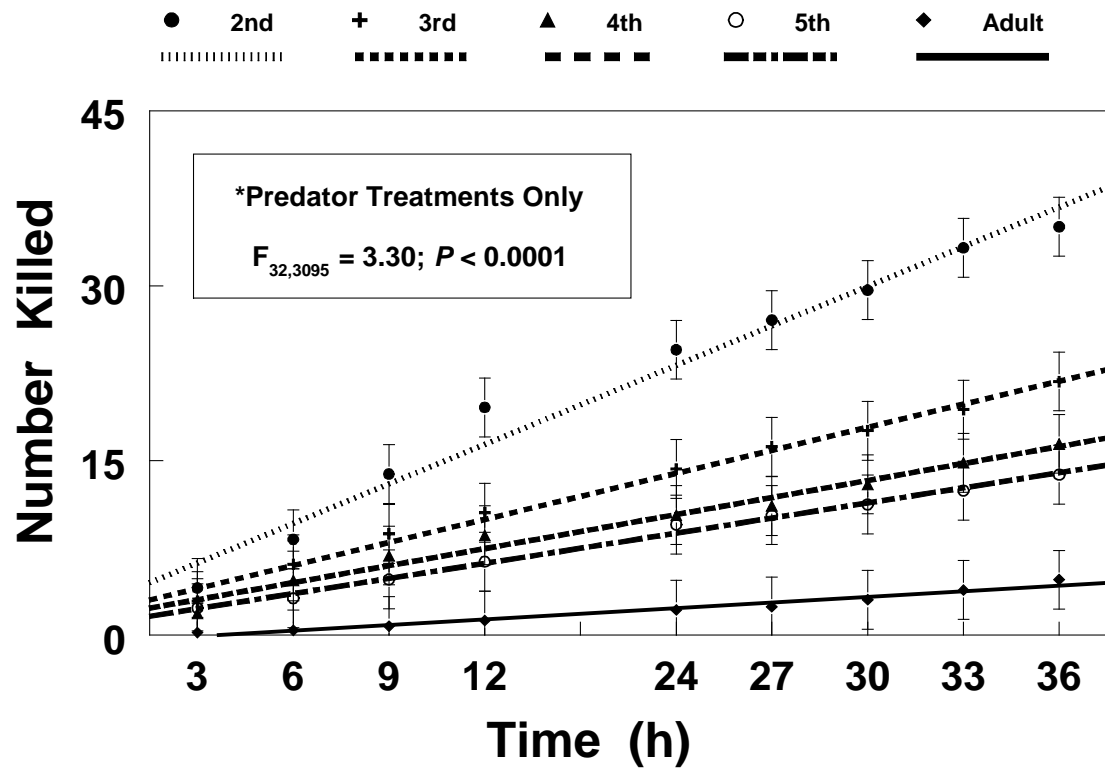


Figure 4. Accumulated number of *Stephanitis pyrioides* killed over 36 h prey – saturation trials, pooled across temperatures, for nymphal and adult stages in the presence of a predator.

***STEPHANITIS PYRIOIDES* DISPERSAL IN THE PRESENCE AND ABSENCE OF PREDATORS**

Significant temperature by predation treatment interactions for *S. pyrioides* dispersal were found for fifth instar nymphs ($F = 23.65$; $df = 2, 561$; $P < 0.0001$) and adults ($F = 4.81$; $df = 2, 561$; $P = 0.0085$). Fifth instars dispersed more often in the predator present treatment at 24°C than at the 18°C and 21°C treatment levels relative to predator absent treatments (Figure 5d). Adults dispersed more often in predator present treatments at 18°C than at 21°C or 24°C (Figure 5e). For the second, third, and fourth instars, predator presence significantly increased prey dispersal ($F = 33.54$; $df = 1, 560$; $P < 0.0001$, $F = 44.96$; $df = 1, 561$; $P < 0.0001$, $F = 32.92$; $df = 1, 561$; $P < 0.0001$, respectively), although there was no effect of temperature (Figure 5a-c).

Examination of the 5x2 (life-stage:predation) factorial revealed a significant life stage by predation interaction ($F = 5.03$; $df = 4, 3,094$; $P = 0.0003$). Early nymphal instar *S. pyrioides* were more likely to disperse in the presence of predators compared to later stages (Figure 6). However, later stages (fifth instars, adults) dispersed more often, independent of predator presence.

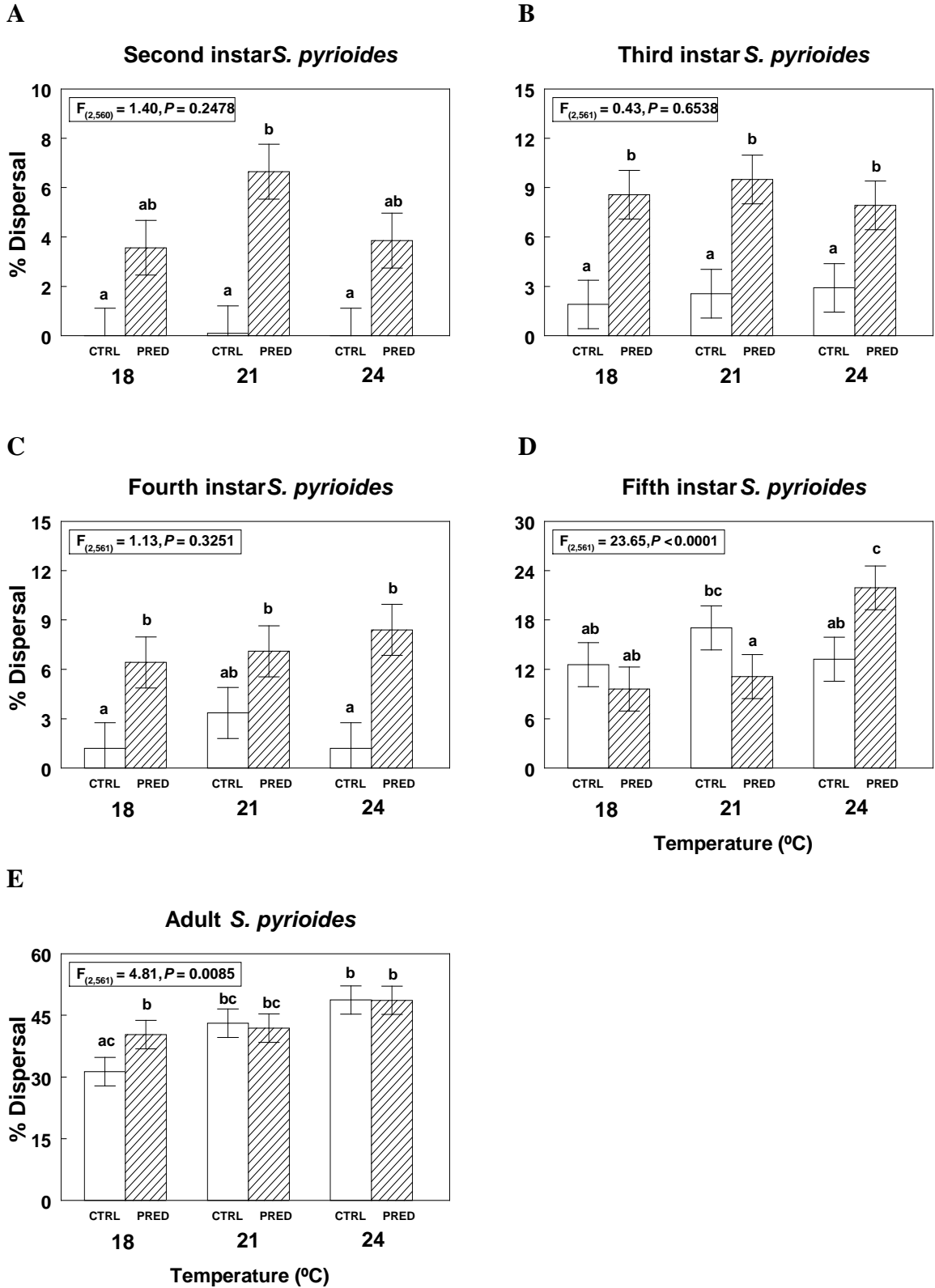


Figure 5. Mean \pm SE *Stephanitis pyrioides* dispersal at three temperatures in predator absent (CTRL) and predator present (PRED) treatments (A-E). Means with the same letter are not significantly different (Bonferroni, $P > 0.05$). Note: y-axes vary.

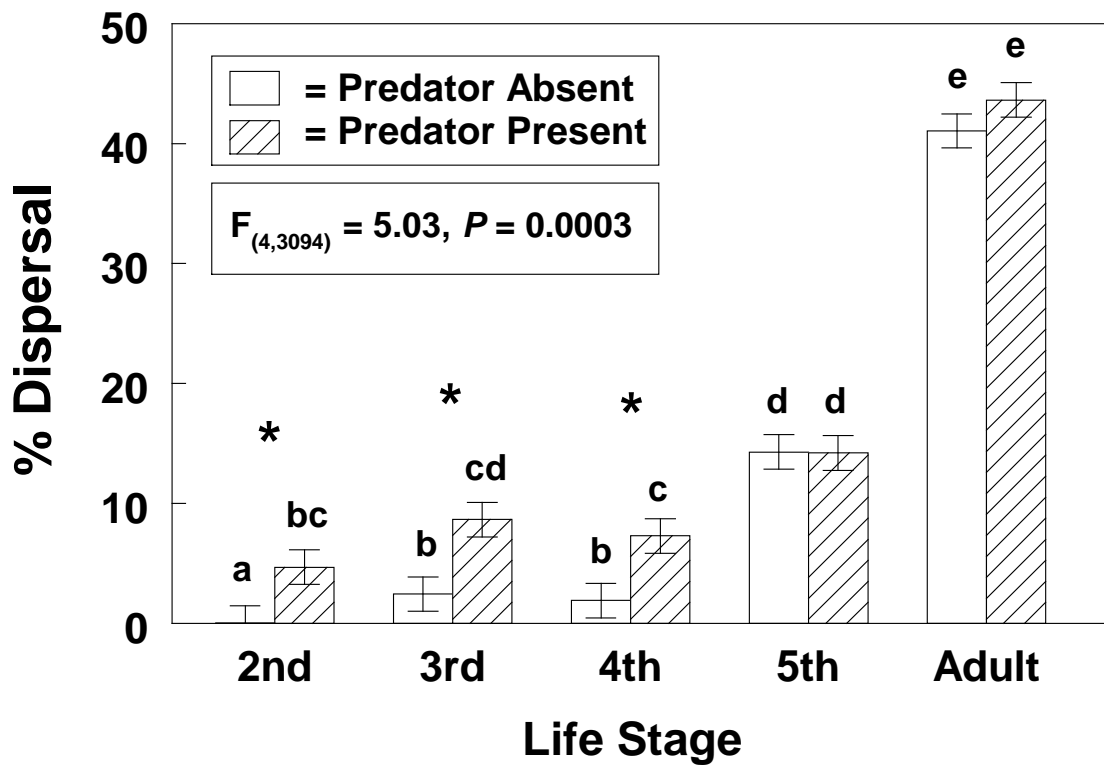


Figure 6. Mean \pm SE *Stephanitis pyrioides* dispersal over 36 h prey – saturation trials, pooled across temperature, for nymphal and adult stages in the presence and absence of a predator. Means with the same letter are not significantly different (Bonferroni, $P > 0.05$). Values with asterisks (*) denote significant differences between predator absent and predator present treatments.

CHRYSOPERLA CARNEA BEHAVIOR

Predator behaviors examined included searching/foraging, feeding, and resting. *Chrysoperla carnea* attack behavior was not observed. Temperature did not significantly influence predator behavior within any prey instar or life-stage ($n = 12$). Probabilities from each Fisher's exact test for the effect of temperature on predator behavior within each prey instar or stage were: second instar ($P = 0.764$), third instar ($P = 0.296$), fourth instar ($P = 0.581$), fifth instar ($P = 0.859$), and adult ($P = 0.852$). In addition, no significant differences between predator behaviors were found between *S. pyrioides* life stages ($\chi^2 = 9.49$; $df = 8$; $P > \chi^2 = 0.303$). During the 36 h period, *Chrysoperla carnea* were most frequently observed resting (88.4%), followed by searching/foraging (6.4%) and feeding (5.1%).

STEPHANITIS PYRIOIDES DEFENSIVE MORPHOLOGY AND BEHAVIOR

Examination of photographic evidence revealed two main lace bug attributes that may pertain to *S. pyrioides* predator-defense as adults. The first includes physical traits that utilize the pronotal hood and mesonotal wing-pair (Drake and Ruhoff 1965). The pronotum covers the head and extends distally beyond the head region as well as mesially to cover sections of the prothoracic leg pair. The mesonotal wing pair forms a flat plane that covers the abdomen and extends laterally beyond the most distal pleurites (Figure 7). The second observed lace bug attribute that may pertain to predator-defense, is a behavioral response to predator probing. *Stephanitis pyrioides* typically maintain an upright posture in the absence of predators and in the presence of predators, if undisturbed (Figure 8a). Upon initiation of *Chrysoperla carnea* probing / attack, adult *S. pyrioides* lower their wings towards the substrate, precluding *Chrysoperla carnea* access

to ventral regions of *S. pyrioides* (Figure 8b-d). *Stephanitis pyrioides* variation in wing pitch (tilt) may be adjusted to reduce *Chrysoperla carnea* access from lateral or posterior points of attack (Figure 8b-d). In addition, *S. pyrioides* tilt positions are braced by leg adjustments when *Chrysoperla carnea* is in contact (Lepping, personal observation). Adult *S. pyrioides* appear to maintain this “tilting” behavior as long as predator probing continues (Lepping, personal observation). Second instar *Chrysoperla carnea* tend to give up probing adult *S. pyrioides* after several seconds and continue searching (Lepping, personal observation). Successful capture of adult *S. pyrioides* by second instar *Chrysoperla carnea* was not observed.

A



B



Figure 7. Ventral view of adult male and female *Stephanitis pyrioides*, respectively (A and B).

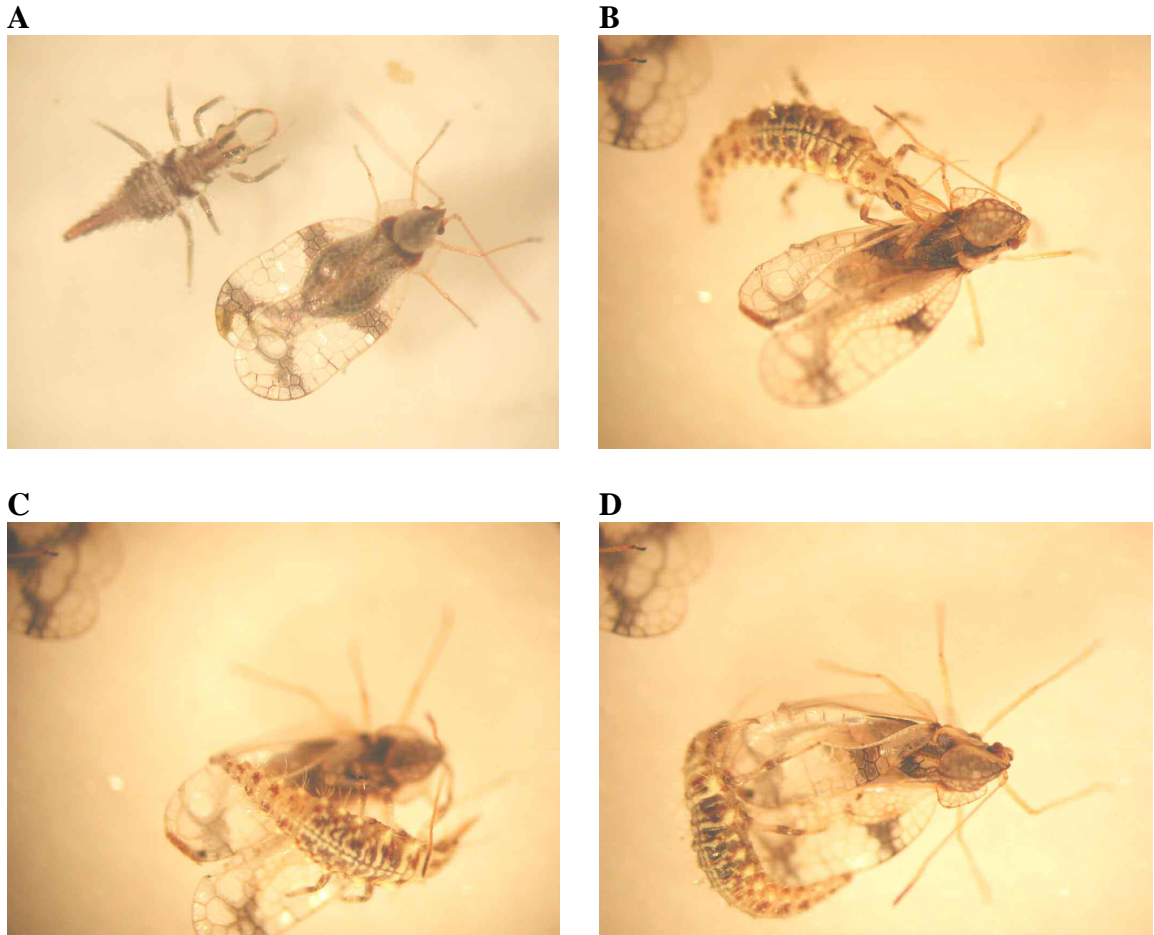


Figure 8. Static (A) and dynamic (B-D) interactions of *Chrysoperla carnea* and *Stephanitis pyrioides*. Note changing orientation of *S. pyrioides* mesonotal wing-plane (pitch) relative to *C. carnea* position before and during probing.

DISCUSSION

This study found that *S. pyrioides* developed slower at lower temperatures. In predation trials using saturated prey densities for nymphal and adult stages of *S. pyrioides*, a significant temperature by life-stage interaction revealed that early instars were consumed more than later instars or adults as temperature increased. Independent of temperature effects, *S. pyrioides* predation was higher for early nymphal stages relative to later nymphal stages, or adults. Behavioral examination revealed that second through fourth instar *S. pyrioides* nymphs dispersed more often when a predator was present than when a predator was absent, relative to fifth instar nymphs and adults. However, fifth instar nymphs and adults dispersed more overall than early nymphal stages.

Overall, early instar *S. pyrioides* required less time to develop than later instars. These findings are consistent with data reported by Neal and Douglass (1988) and Braman et al. (1992). Lower developmental thresholds (T_o) and degree-day requirements (K) found in this study for discrete nymphal stages were slightly dissimilar to those reported by Braman et al. (1992) for *S. pyrioides* development on the same azalea species and cultivar, using similar temperature treatments. However, the 12.2°C developmental threshold for second instar through fifth instar nymphal development reported here matches that found for first instar through fifth instar nymphal development in their study. Differences in methodology (e.g. variation in host-plant material or variation in endemic *S. pyrioides* populations from distinctly different temperature zones) may explain observed differences at the instar level.

Stephanitis pyrioides developed more slowly in lower temperature environments. Not surprisingly, similar effects of temperature on *S. pyrioides* development were found

by Braman et al. (1992) in laboratory studies and Shrewsbury (1996) in an urban landscape environment. Stage-specific mortality from predation decreased for successively later stages, demonstrating that early instar *S. pyrioides* are more vulnerable to predation than later life stages. Therefore, slow development of *S. pyrioides* in cool environments may result in *S. pyrioides* remaining in vulnerable life stages for extended periods. Temperature mediated variation in growth-rate dependent vulnerabilities to predation may, in part, be due to differences in molting period (Stamp 1990, Stamp and Bowers 1990). Although this study did not determine *S. pyrioides* molting time, temperature-dependent vulnerabilities during nymphal ecdysis are likely, as *S. pyrioides* nymphs appear to be incapable of dispersal or other defensive behaviors during and shortly after ecdysis (Lepping, personal observation).

In addition to temperature affecting *S. pyrioides* development, predator activity may also be temperature dependent, as predator-inflicted mortality decreased as temperature decreased. In accord with these findings, El-Wakeil (2003) reported decreased *Chrysoperla carnea* consumption rate with decreasing temperature. Therefore, slowed growth of *S. pyrioides* in cool environments may not necessarily translate into greater predation. Exposure to predation, or the time predators are actively foraging on vulnerable *S. pyrioides* life stages, may also be lower for vulnerable stages of *S. pyrioides* at lower temperatures.

Predator – prey interaction studies that examine prey vulnerability and / or exposure have typically included variables such as host-plant quality that directly influence prey performance and therefore prey vulnerability to natural enemies (Benrey and Denno 1997, Gross and Price 1988). However, previous studies have mainly focused

on variables that do not necessarily produce strong direct effects on natural enemy activity, such as temperature in the present study. Nonetheless, Benrey and Denno (1997) note that studies examining prey vulnerability (as it pertains to variation in host-plants) should include a statement about host-plant architecture, as variation in plant morphology across host-plants may directly influence natural enemy searching behaviors and subsequent enemy success (Evans 1976, Kareiva and Perry 1989, Murdoch et al. 1989, Clark and Messina 1998). Although this study did not directly measure exposure, the frequency of predator behaviors (foraging, feeding, resting) did not differ among temperature treatments. However, lack of significant differences for predator behaviors may be due to large intervals between sampling, resulting in minimal observation time.

Several potential direct effects of temperature on predators or prey may obscure prey vulnerability and exposure to predation (Anderson et al. 2001). Direct temperature effects may influence prey detection of natural enemies, alarm signaling, escape behaviors and/or defense (Gilchrist 1995), as well as predator foraging (Dreisig 1981, Morgan 1985), prey handling (Thompson 1978), and metabolism (Schultz et al. 1992). Although the present study did not examine all of these factors, prey dispersal in the absence of a predator was found to slightly increase for *S. pyrioides* adults as temperature increased. Later life stages of *S. pyrioides* may be less bound to their host plant than early life stages for nutritional resources as the reproductive stage is reached, and tendency for dispersal could then be influenced by temperature. This suggests that temperature could directly influence *S. pyrioides* response to predator presence.

In addition to the direct effects that temperature may have on predators and prey, prey vulnerability and exposure to predation are likely influenced by the interactions of

predator and prey responses to thermal environment. That is, predator- and prey-specific responses to identical thermal environments may create asynchronous effects on predator and prey activity (Stamp et al. 1997, Anderson et al. 2001, Roy et al. 2002). Herbivore species-specific thermal requirements may dictate optimal developmental temperatures and potentially temperature-dependent responses to predator presence. Similarly, predator species-specific thermal requirements may dictate optimal ranges for prey discovery and consumption. The magnitude and direction of the resultant asynchrony may confer a potential advantage to either predator or prey. For example, previous studies have identified the larval developmental threshold for *Chrysoperla carnea* as 8.3°C (Butler and Ritchie 1970), and the nymphal developmental threshold for *S. pyrioides* as 12.2°C (Braman et al. 1992, Lepping Chapter 1). A lower developmental threshold for the predator suggests that *Chrysoperla carnea* may be active in thermal environments where *S. pyrioides* may not be able to fully respond with escape and/or defensive behaviors. Moreover, predators that exhibit thermoregulatory behaviors or possess broad or plastic operational temperature ranges may be able to forage in varying thermal environments without suffering significant losses in efficiency (Gilchrist 1995, Schultz 1998).

Asynchronous responses to a common thermal environment by predator and prey may extend beyond immediate actualization and influence developmental asynchronies and / or temporal synchronicity of predator and prey populations (Neal and Haldemann 1992, Anderson et al. 2001, Roy et al. 2002). For example, asynchrony in seasonal egg hatch of the tingid-specialist predator *Stethoconus japonicus* (Heteroptera: Miridae) and

S. pyrioides populations may influence temporal *S. pyrioides* exposure at the population level (Neal and Haldemann 1992).

For immature ectothermic predators operating in a range of environmental temperatures between the lower developmental threshold and the median point of an optimal developmental range, one may expect prey consumption to be more frequent in warmer ranges when compared to cooler ranges. For example, Islam and Chapman (2001) examined the effects of constant and fluctuating thermal regimes on the developmental and predation rates of the Tasmanian lacewing, *Micromus tasmaniae* (Walker) (Neuroptera: Hermerobiidae) a natural enemy of the cabbage aphid, *Brevicoryne brassicae* (Linnaeus) (Sternorrhyncha: Aphididae). Constant temperature treatments ranged from 10 to 30°C, with 5°C stepwise intervals; fluctuating temperatures ranged from 10 to 25°C. Lacewing larval developmental time decreased and predation increased linearly with temperature. Under fluctuating thermal regimes, development and predation were similar to those found at a constant temperature of 25°C. Similarly, El-Wakeil (2003) found *Chrysoperla carnea* larval development time to decrease and consumption rate to increase with increasing temperature (20, 25, and 30°C). In greenhouse studies of *Chrysoperla carnea* response to thermal environment, Sundby (1966) found predation on the green peach aphid, *Myzus persicae* (Sternorrhyncha: Aphididae), to increase 32% as temperature increased from 16 to 21°C. Similarly, Scopes (1969) found *Chrysoperla carnea* predation on *M. persicae* to increase 10% as temperature increased from 15 to 21°C.

Maximum operational temperatures are also important in predator activity (Schultz et al. 1992). If environmental temperatures exceed critical thresholds,

deleterious and potentially lethal effects begin to occur (Pearson, and Lederhouse 1987, Ba M'Hamed and Chemseddine 2001, Canard and Volkovich 2001), and predator activity and / or prey consumption may be reduced (Tulisalo 1984). In this study, overall predation of *S. pyrioides* by *Chrysoperla carnea* did not decline as temperature increased, indicating that the warmest thermal regime tested (24°C) is likely below the critical threshold for *Chrysoperla carnea* activity.

In this study, significant temperature by life-stage interactions revealed that predation was greater in warmer environments, especially for early instar *S. pyrioides*. Greater predation by *Chrysoperla carnea* at 21 and 24°C relative to 18°C may indicate that the higher temperatures are points in the optimal temperature range for predator performance. Warmer environments may increase *Chrysoperla carnea* metabolic requirements and induce predator searching, whereas in sub-optimal thermal environments these activities may be delayed or retarded (El-Wakeil 2003). In natural habitats, warmer environments may potentially allow *Chrysoperla carnea* to consume *S. pyrioides* at rates that would negate or offset any benefit gained by *S. pyrioides* developing faster in warmer environments (Genden and Axtell 1988). However, the general observation of greater *S. pyrioides* abundance in exposed, high light habitats, suggests that this negation is unlikely, or that other factors are also influencing *S. pyrioides* distribution patterns.

Independent of temperature effects on predation, prey saturation studies allowed for an estimate of potential maximum predation rates of *S. pyrioides*. In this study, decreasing predation rates were observed for two of the four nymphal instars examined. Predation rates at the end of the 36 h sampling period were low relative to initial

Chrysoperla carnea predation rates. For discrete prey stages, decreasing predation rates by this type-2 predator (Bond 1980, Stewart et al. 2002) may indicate that the predator is becoming satiated. Satiation for a discrete larval instar may indicate that metabolic requirements have been met for the instar, and/or ecdysis will soon occur (Canard et al. 1984, Lepping, personal observation).

For adult *S. pyrioides* in the prey saturation experiment, capture rate was found to increase slightly, from $\cong 0$ to 1 individuals in a 36 h period. This finding suggests that adult *S. pyrioides* are inaccessible to *Chrysoperla carnea* and that they may have defensive mechanisms that reduce attack efficiency of *Chrysoperla carnea*. *Chrysoperla carnea* may acquire greater nutritional resources by garnering larger *S. pyrioides*, capture success may be greater, and therefore nutritionally better, for smaller prey (Roger et al. 2000, Cogni et al. 2002, Venzon et al. 2002).

Differential mortality between second instars, the third/fourth/fifth instar class and adults raises questions about the mechanism(s) that influence *S. pyrioides* vulnerability to predation. *Stephanitis pyrioides* vulnerability to predation may be influenced by behavioral- or morphology-based mechanisms, or a combination thereof. The present study examined *S. pyrioides* dispersal as a potential behavioral mechanism to explain *S. pyrioides* life-stage specific vulnerability to predation.

Overall dispersal of *S. pyrioides*, in the absence of predators, tended to increase for later instars and the adult stage. Greater dispersal with increased age may be expected for *S. pyrioides*. As size increases dispersal capabilities may develop, whereas for immature stages mobility may be a limiting factor. However, early instars dispersed more often when in the presence of a predator, whereas dispersal of later life stages of *S.*

pyrioides was already high and not influenced by the presence of a predator. Greater vulnerability to predation may drive early stages of *S. pyrioides* to adopt dispersal tactics when predators are present. Although this study did not examine intra-species interactions, alarm signaling or related chemical signals may have facilitated nymphal dispersal, as related lace bug species have been found to elicit alarm pheromones that stimulate dispersal (Aldrich et al. 1991). Life history traits, such as age-specific dispersal behaviors, may in part be associated with life stage vulnerability and potential tradeoffs in survival.

Differential vulnerability to predation between life stages of *S. pyrioides* may also be influenced by physical defenses. The physical characteristics *S. pyrioides* possess may be employed beyond simple shielding through a “tilting” behavior. The “tilt defense” mechanism may enable adult *S. pyrioides* to avoid predation after initial discovery by predators. A combination of defensive armature and tilting behavior may partially explain reduced mortality of adult *S. pyrioides* relative to nymphal stages. Examination of these traits for the hawthorn lace bug, *Corythucha cydoniae* (Fitch) and the green lacewing, *Chrysoperla rufilabris* (Burmeister) revealed similar results (Lepping, personal observation).

Addressing similar questions, Tallamy and Denno (1981) conducted one of few studies specifically examining vulnerability of tingids to predation as mediated by nymphal defenses. In their study, two lace bug species possessing contrasting nymphal morphology were exposed to lady beetles (Coleoptera: Coccinellidae) and lacewings. Under lady beetle predation, the more spinose and strongly sclerotized lace bug species were consumed significantly less than the weakly sclerotized species. However, when

exposed to lacewing larvae, both herbivore species were consumed equally. Tallamy and Denno (1981) suggest that while chewing predators, such as lady beetles, may ineffectively attack lace bug nymphs with complex spine morphologies, piercing – sucking predators, such as lacewings, may penetrate these defenses.

In a related study, Shrewsbury and Lepping (unpubl.) found reduced predation of later, more developed stages of *Corythucha cydoniae* when in the presence of the green lacewing, *Chrysoperla rufilabris*. They found early nymphal stages of *Corythucha cydoniae* to be significantly more vulnerable to predation than later nymphal stages, or adults. This pattern in life-stage vulnerability is similar to that found in the present study of *S. pyrioides*. For both lace bug species, spine number and size increase with increasing nymphal stages (Lepping personal observation); upon adult eclosion, spine morphology is replaced with expanded and sclerotized pronotal and wing structures which bear reticulate (latticed) venation from which the common name “lace bug” is derived (Drake and Ruhoff 1965). In accord with Tallamy and Denno (1981), these studies support findings that nymphal defense characteristics of lace bug may not significantly reduce susceptibility to lacewing predation. Conversely, late instar nymphs and adult lace bug, which appear to have greater morphological defenses relative to nymphs, suffer less mortality than nymphs under lacewing predation.

This study found increased predation, especially of early instars, at warmer temperatures, suggesting *S. pyrioides* may be more susceptible to predation in warm habitats such as sunny exposed habitats. However, this study clearly demonstrates the greater vulnerability of early *S. pyrioides* instars than later to predation, regardless of

temperature. This study finds that differences in life-stage have a greater impact on predation of *S. pyrioides* than temperature. It may be inferred that lace bug in cooler habitats, such as shady landscapes, develop more slowly and therefore remain in vulnerable life stages longer than lace bug in warmer, exposed habitats. These studies support the findings of Shrewsbury (1996) where predators more effectively suppress *S. pyrioides* in cooler, more structurally complex habitats. The combination of being subject to longer periods of vulnerability and predator abundance being greater in complex habitats (Shrewsbury 1996) may explain patterns of *S. pyrioides* abundance in urban landscapes.

In the context of basic insect ecology, this work addressed the question of how a governing environmental component, temperature, may influence predator – prey interactions. The findings of this work may also translate directly into applied usage for pest management considerations. This study examined the effects of thermal environmental variation on pest development and susceptibility to predation. The developmental data for *S. pyrioides* allows for degree-day based life-stage tracking, and therefore may aid in pest management decision making oriented to targeting pests in vulnerable stages. Pest managers identifying vulnerable *S. pyrioides* life stages may then estimate periods that biological control tactics may be efficacious, as well as periods that alternative controls may be necessary.

Chapter II

Stephanitis pyrioides development and vulnerability to predation by *Chrysoperla carnea* in shaded and non-shaded habitats

ABSTRACT

Differential thermal environments, created by abiotic shade structures, were examined for their influence on the performance and fitness of a specialist pest, the azalea lace bug, *Stephanitis pyrioides* (Scott) (Heteroptera: Tingidae).

A 1.4°C temperature differential between environments resulted in a 2.7 d developmental lag for *S. pyrioides* in shaded, cooler, northern exposure habitats as compared to those in exposed, warmer, southern exposure habitats. Habitat exposure did not influence oviposition rates between habitats during field studies. Thermal environment also did not generally influence predation by the green lacewing, *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae) on nymphal and adult stages of *S. pyrioides*. Trends in *S. pyrioides* life-stage specific vulnerabilities to predation suggest decreased predator-inflicted mortality for later stages of *S. pyrioides*.

This study supports previous laboratory findings of slower *S. pyrioides* development in cooler environments, as well as greater vulnerability to predation for early instars relative to later instars, or adults. *Stephanitis pyrioides* develop more slowly in shaded, cool habitats, thereby increasing periods that populations are in more vulnerable stages. Conversely, herbivore populations developing in exposed, warm habitats may enter less vulnerable stages faster than those in the shade, thereby reducing the likelihood of predation.

This work underscores the necessity for landscape pest monitoring, as the success of an IPM program utilizing conservation or augmentative biological control is dependent on targeting key pests in vulnerable stages.

INTRODUCTION

Numerous studies have examined the influence of vegetational texture on, and the mechanisms underlying, patterns in herbivore and natural enemy distribution and abundance (Tahvanainen and Root 1972, Root 1973, Bach 1980a and b, 1981, 1986, 1988, Kareiva 1983, Sheehan 1986, Russell 1989, Letourneau 1990a and b, Hanks and Denno 1993, Denno 1994, Shrewsbury and Raupp 2000, Tooker and Hanks 2000). Vegetational texture has been described in terms of plant density, patch size, and vegetational diversity (Kareiva 1983, Denno and Rodderick 1991). From the principle components of vegetational texture we may derive other measurements of a habitat. These include architectural and/or structural complexity, plant species diversity, evenness, richness, plant density and growth form, color contrasts, volatile plant compounds, and intra-species genotypes (Letourneau 1990a, Andow 1991). Differences in vegetational texture can also influence levels of light exposure (Risch 1981, Andow 1991, Shrewsbury 1996). Several studies have demonstrated that herbivore abundance and plant injury are greater in sunny, exposed habitats, compared to shadier, more natural habitats (Raupp 1984, Hajek and Dahlsten 1986, Louda et al. 1987, Collinge and Louda 1998, Moore et al. 1988, Cappuccino and Root 1992, Trumbule and Denno 1995, Trumbule et al. 1995, Louda and Rodman 1996, Shrewsbury and Raupp 2000).

Within the family Tingidae (Heteroptera), studies have examined the influence of vegetational texture and related habitat components on lace bug fitness, performance, and distribution (Cappuccino and Root 1992, Trumbule and Denno 1995, Trumble et al. 1995, Shrewsbury 1996, Shrewsbury and Raupp 2000). Azalea lace bug, *Stephanitis pyrioides* (Scott) (Heteroptera: Tingidae) is a specialist of azaleas (*Rhododendron* spp.) and has been identified as a prominent pest in commercial and private landscapes throughout Maryland (MD), U.S. (Raupp and Noland 1984). *Stephanitis pyrioides* has been observed to infest and damage azaleas located in sunny, exposed habitats more frequently than those in shady, more natural habitats (Raupp 1984, Trumbule et al. 1995, Trumbule and Denno 1995, Shrewsbury 1996, Shrewsbury and Raupp 2000). Alternatively, other studies report greater *S. pyrioides* abundance in shaded habitats, or no difference in *S. pyrioides* abundance between shaded and non-shaded nursery-like environments.

Shrewsbury and Raupp (2000) examined multiple components of vegetational texture and their influence on *S. pyrioides* populations in ornamental landscape settings. They found that structural complexity (frequency of vegetation in five distinct strata of a three dimensional patch) best explained patterns in lace bug abundance. Of the five vegetational strata that were measured for each site, 71% of the variation in azalea lace bug abundance was due to the presence or absence of an overstory layer (Shrewsbury and Raupp 2000). In landscapes with low structural complexity, and little overstory, lace bug abundance was greater than landscapes with high structural complexity (Shrewsbury and Raupp 2000). Following structural complexity, light exposure best explained greater lace bug abundance in structurally simple landscapes than complex (Shrewsbury and Raupp

2000). Azalea in structurally simple habitats, that lacked understory or overstory layers, received greater periods of light exposure. Conversely, azalea in structurally complex sites were found to receive less direct sunlight. Shrewsbury (1996) also determined that structurally simple habitats were $\cong 2.5^{\circ}\text{C}$ warmer than complex habitats. Differences in light exposure likely translated to differences in temperature. Moreover, structurally complex sites supported fewer *S. pyrioides*, higher natural enemy diversity and abundance, and greater predation of *S. pyrioides* (Shrewsbury 1996).

Differential thermal environments may influence development of herbivores (Neal and Douglass 1988, Stamp and Bowers 1990, Stamp et al. 1997, Braman 1992, Braman and Pendley 1993, Milonas and Savopoulou-Soultani 2000, Sipura and Tahvanainen 2000, Lepping Chapter 1) and the period of time life stages are vulnerable to natural enemies (Shrewsbury 1996, Lepping Chapter 1, Lepping and Shrewsbury unpubl.). For example, Shrewsbury (1996) found that degree-day accumulations were lower and *S. pyrioides* development slower in structurally complex landscapes relative to simple ones. In a laboratory study, Lepping (Chapter 1) examined the effects of three constant thermal regimes (18°C , 21°C , 24°C) on *S. pyrioides* development and vulnerability to predation by the green lacewing, *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae); a generalist predator commonly found in association with *S. pyrioides*. In that study, *S. pyrioides* nymphal developmental time increased with decreasing temperature. Development of *S. pyrioides* was protracted by approximately 7 d for each 3°C difference in environmental temperature. However, predation also decreased as temperature decreased, suggesting that direct effects of temperature may also reduce predator activity in low temperature thermal environments. *Stephanitis*

pyrioides mortality in the presence of a predator was also found to be higher for early nymphal stages compared to later nymphal stages or adults. That study identified differences in *S. pyrioides* life-stage vulnerability to predation and differences in development.

Lepping (Chapter 1) suggested that slowed or delayed development of vulnerable *S. pyrioides* life stages may result in longer periods of vulnerability to predation, especially where thermal environment has asynchronous effects on predator and prey. Predators that possess lower developmental thresholds than their prey, or broad or plastic operational temperature ranges, may suffer reduced penalties when foraging in lower temperature environments (Lepping Chapter 1). Trumbule and Denno (1995) suggested that altering abiotic factors, such as increasing light exposure and / or temperature, or decreasing ambient moisture levels might discourage natural enemies of *S. pyrioides* from entering azalea patches. The resulting vegetational texture of a habitat may then indirectly affect herbivore distribution by influencing predator abundance and / or composition (Riechert and Tracy 1975, Kareiva 1987, Murdoch et al. 1989, Dobel and Denno 1994, Dyer and Landis 1997).

To further the research of Trumbule and Denno (1995), Shrewsbury and Raupp (2000), and Lepping (Chapter 1), and to identify possible mechanisms underlying observed patterns in lace bug abundance, this study examined the influence of thermal variation, through a shading effect, on the performance and fitness of *S. pyrioides*, in the presence and absence of natural enemies. The specific objective of this study was to determine the effect of varying light exposure / thermal environment on *S. pyrioides* development and vulnerability to predation.

METHODS

EXPERIMENTAL FIELD DESIGN

Field studies were conducted at the Central Maryland Research and Education Center (C.M.R.E.C), in Upper Marlboro, Prince Georges County, MD. Each of five whole-plots (replicates) measured 2.4 m long by 2.4 m wide (Figure 1) and were positioned no less than 30 m from one another. For each replicate, wall structures were constructed to create a shade effect for northern exposure sub-plots and a sun effect for southern exposure sub-plots. Wall structures measured 3.2 m high by 2.4 m wide, and were oriented along an east-west transect. Within whole-plot ground cover consisted of bare soil, surrounding areas consisted of 0.5 m high ground cover (tall fescue, *Festuca arundinacea* (Schreber) (var. Kentucky-31) (Cyperales: Poaceae)). Each wall consisted of composite 15.2 cm thick cinder block (from soil surface to 1.5 m) and 2.0 cm thick particle board (from 1.5 to 3.2 m). All wall surfaces were painted with white, outdoor paint to increase reflective properties.

Forty azalea plants were arranged in groups of eight, and split between northern and southern exposure environments (sub-samples) (Figure 1). Host-plant patches were established 0.3 m from, and centered in respect to the wall length, to reduce edge effects. Individual plant canopies did not contact one another. Study plants consisted of 2 year-old azalea, *Rhododendron mucronatum* (Blume) G.Don (var. Delaware Valley White) (Ericaceae: Rhododendron), obtained from a commercial nursery and maintained under uniform growing conditions until treatment assignment. Plant canopies measured approximately 38.1 cm in diameter and were situated in a pot-in-pot arrangement. “Pot-in-pot” is defined as sinking a planter into the soil, and inserting a potted plant into the

sunken planter. The pot-in-pot arrangement supports consistent maintenance and controls for soil variation in field studies. Plots were arranged to reduce factors contributing to environmental biases, including: positioning to minimize local wind pattern interference and adjacent vegetational or non-vegetational shading effects. Irrigation was delivered as needed via manual soil drenching.

EFFECTS OF EXPOSURE ON HABITAT TEMPERATURE

The wall structure acts as a barrier to radiant sun energy in the forms of infrared radiation, visible light, and ultra-violet light, for northern exposure sub-plots. Alternately, the reflective properties of the wall surface were expected to refract visible and ultra-violet light into southern exposure sub-plots, thereby potentially increasing microhabitat temperatures. In addition to refractive energy exposure, convective heat exchange may have occurred between wall surfaces and study plants.

To determine if habitat temperatures differed between the northern and southern exposures, temperature measurements were recorded at 24 min intervals over the course of study with electronic, double-probe data loggers (HOBO H8 Pro, Temperature / External Temperature P/N: H08-031-08, Onset Corporation, Bourne, MA.). A pair of data loggers were split over whole-plot treatments and arranged to record intra-canopy and inclusion-cage temperatures (to test for cage-effects). Each data logger base probe was positioned 0.45 m from the shade structure, within the plant canopy. Remote probes were tied to inter-cage branches such that they lay the same distances from the wall and soil-surface as the base-probe.

STEPHANITIS PYRIOIDES DEVELOPMENT AND SURVIVAL IN THE ABSENCE OF PREDATORS

Stephanitis pyrioides used in field experiments were collected from a single field population in College Park, MD. Cohorts of 20, second instar lace bug nymphs, were transferred individually to new growth of branches on azaleas using a camel hair paintbrush. A single cohort was introduced to each of the four sub-sample host-plants in each exposure, and confined by inclusion cages. Cages were made from mylar sheets formed into tubes measuring 15 cm long by 5 cm in diameter. Each tube cage had 3.8 cm² openings on opposite sides, which were covered with a lightweight mesh cloth to allow airflow. Tube cages were sealed and attached to branches using foam plugs (*from* Shrewsbury 1996). Five replicates were arranged as a randomized complete block design. *Stephanitis pyrioides* cohorts were monitored with visual observations *in situ* once daily for *S. pyrioides* survival and life-stage, starting on 1 May 2003, until all cohort members either disappeared, died, or eclosed to adult.

STATISTICAL ANALYSIS

Mean values for nymphal survival of each instar were estimated from the maximum number of individuals recorded for a successive instar or stage. Overall nymphal survivorship was calculated from the means of instar survival, whereas sub-total nymphal survivorship was based on the maximum number of adults recorded. Mean values for duration of development for each instar were calculated from the proportion of surviving individuals in a given instar per day (proportional days), and summed over all days that any cohort member was in the given instar. Environmental temperatures, nymphal survival, and duration of nymphal development were compared across exposure habitats using the MIXED procedure and bonferroni test (SAS Institute 2003). All

ANOVA procedures included the Kenward – Roger method for calculation of degrees of freedom, and maximum experimentwise error rates were limited with Bonferroni tests for all multiple mean comparisons (SAS Institute 2003).

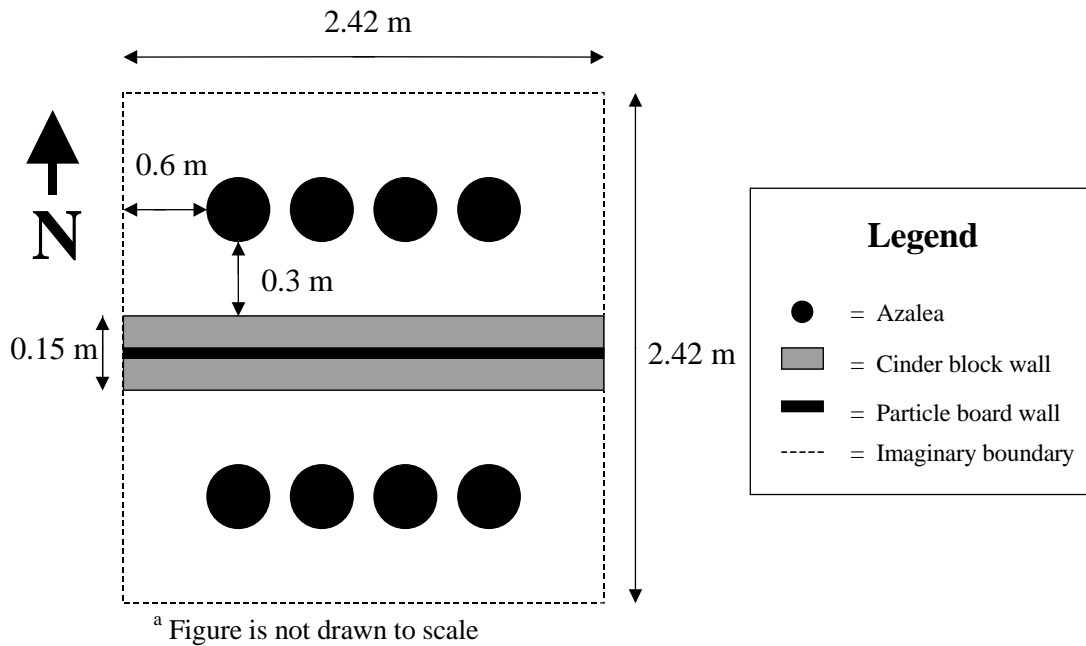


Figure 1. Experimental design for field experiments (1 replicate / block = whole plot)^a.

***STEPHANITIS PYRIOIDES* SURVIVAL IN THE PRESENCE AND ABSENCE OF PREDATORS**

Inclusion cages and lace bug cohorts in the predator experiment were arranged as per the development experiments described above, with the following adjustments. *Stephanitis pyrioides* instars two, four, five, and the adult stage were examined in experimental field plots in temporal synchronicity with the endemic source population. Dates of predation trials for each *S. pyrioides* nymphal or adult stage were: second instar (04/31/2003-05/03/2003), fourth instar (05/14/2003-05/17/2003), fifth instar (05/19/2003-05/22/2003), and adult (06/02/2003-06/05/2003). Vulnerabilities of specific life stages to predation were examined discretely to enable comparison of predator inflicted mortality and duration of development for each nymphal instar between northern and southern exposure habitats.

For the second instar, a single cohort of 20 *S. pyrioides* nymphs was introduced to each of the four sub-sample host-plants in each exposure, whereas only two sub-sample host plants were used for instars four and five, and the adult stage, as *S. pyrioides* availability was limited. For each nymph or adult experiment, 5 replicates were arranged as a randomized complete block, split-plot design with a 2x2 factorial treatment structure (exposure:predation). Whole plots included two treatment exposures (northern/southern); sub-plots included a predator treatment (predator absent or predator present).

The predator treatment was provided by introducing a single, second-instar *C. carnea* (Rincon Vitova Insectiaries, Inc., Ventura, CA) into inclusion cages approximately 1 h after prey infestation. A lacewing density of one was chosen to eliminate the potential for cannibalism (Canard and Duelli 1984). Predator and prey

densities were monitored with visual observations *in situ* once daily for 3 days. At the first and second sampling intervals, missing or dead predators were replaced.

STATISTICAL ANALYSIS

Each life-stage 2x2 (exposure:predation) factorial for prey survival was examined using the repeated measures design with a compound symmetry covariate structure. All ANOVA procedures included the Kenward – Roger method for calculation of degrees of freedom, and maximum experimentwise error rates were limited with Bonferroni tests for all multiple mean comparisons (SAS Institute 2003).

***STEPHANITIS PYRIOIDES* FECUNDITY IN THE ABSENCE OF PREDATORS**

Additional measures of differential habitat exposure / thermal environments on *S. pyrioides* include potential effects on adult fecundity (fitness). To determine lace bug fecundity, two laboratory-reared female and male azalea lace bug adults were randomly assigned to branches (\cong 15 cm in length) in inclusion cages on each sub-sample plant in both exposures. Adult cohorts were left to oviposit for 8 d intervals throughout the fecundity experiment. The fecundity trial ran for 40 days (05/01/2003 – 06/10/2003). At the end of each 8 d interval, cohorts of adults were moved to new branches; missing or dead adults were replaced from lab colonies. Branches from which adults were moved, were removed from sub-sample plants, returned to the laboratory, and evaluated for *S. pyrioides* egg density. Egg densities for each branch were determined by removing frass from the underside of all leaf surfaces, backlighted, and scored for the number of eggs per female per 8 d interval (fecundity).

STATISTICAL ANALYSIS

Fecundity in northern and southern exposure habitats were examined for differences using a repeated measures design with compound symmetry covariate structure, the Kenward – Roger method for calculation of degrees of freedom, and maximum experimentwise error rates were limited with Bonferroni tests for all multiple mean comparisons (SAS Institute 2003).

RESULTS

EFFECTS OF EXPOSURE ON HABITAT TEMPERATURE

The wall structure created a shading effect by blocking direct sunlight for all northern exposure plants from $\cong 0500$ hours (sunrise) until $\cong 1300$ hours each day. Therefore, southern exposure plants received direct sun exposure for an additional $\cong 8$ h during morning periods, compared to northern exposure plants, when cloud cover did not preclude sunlight. Temperatures in northern and southern exposure treatments are presented with the results of respective experiments. In examining for inclusion cage effects on temperature within each exposure treatment, there were no significant differences within plant canopies with cages and without ($F = 5.12$; $df = 1, 4$; $P = 0.0686$) (development/survival/fecundity). Over the course of nymphal development experiments (05/01/2003-06/09/2003), inclusion-cage temperatures in southern exposure habitats were $1.4 \pm 0.1^\circ\text{C}$ warmer than those in northern exposure habitats (Table 2).

***STEPHANITIS PYRIOIDES* DEVELOPMENT AND SURVIVAL IN THE ABSENCE OF PREDATORS**

Stephanitis pyrioides nymphal survivorship was not significantly different between exposures for within each instar or across instars ($F = 1.01$; $df = 1, 34$; $P =$

0.3212). Relative to the initial cohort size of 20 individuals, mean survival was 12.6 ± 1.0 in the northern exposure, and 13.5 ± 1.0 in the southern exposure at any one point during development. Statistical values for each nymphal instar include: the second ($F = 0.83$; $df = 1, 4$; $P = 0.4130$), third ($F = 1.52$; $df = 1, 4$; $P = 0.2845$), fourth ($F = 0.15$; $df = 1, 4$; $P = 0.7225$), and fifth ($F = 0.41$; $df = 1, 8$; $P = 0.5376$). Sub-total nymphal survival was approximately 50%, as measured by maximum adult eclosion (Table 1).

Time required for the development of second instars was the least, whereas fifth instars required the longest time (Table 2). Significant differences in duration of development between exposures occurred for the second ($F = 98.56$; $df = 1, 4$; $P = 0.0006$) and fourth instars ($F = 7.90$; $df = 1, 8$; $P = 0.0228$). Statistical values for instars that were not significantly different between exposures include: the third ($F = 0.31$; $df = 1, 4$; $P = 0.6092$) and fifth ($F = 1.89$; $df = 1, 8$; $P = 0.2060$). Time required to complete development from mid-second instar through adult eclosion was 2.7 ± 1.0 d longer in northern exposure habitats than southern exposure habitats ($F = 7.34$; $df = 1, 8$; $P = 0.0267$).

Table 1. Mean \pm SE survival of *S. pyrioides* on 'Delaware Valley White' azaleas in northern and southern exposures of field plots with natural enemies excluded

Instar	Exposure ^a	
	Northern	Southern
2	15.5 \pm 0.6a	16.0 \pm 0.6a
3	12.6 \pm 1.0a	13.9 \pm 1.0a
4	12.8 \pm 1.7a	13.4 \pm 1.7a
5	9.4 \pm 1.3a	10.6 \pm 1.3a
Sub-Total Nymphal	9.4 \pm 1.3a	10.6 \pm 1.3a

Means followed by the same letter within a row are not significantly different ($P > 0.05$, Bonferroni test).

^a Initial cohorts were comprised of 20 second instar nymphs per plant (sub-sample). Values are the means of individuals completing each instar for each cohort.

Table 2. Mean \pm SE duration of development of *S. pyrioides* on 'Delaware Valley White' azaleas with natural enemies excluded, and associated thermal environments in northern and southern exposures of field plots

Instar	Development, Days ^a		Temperature, °C	
	Northern	Southern	Northern	Southern
2	2.6 \pm 0.1a	2.0 \pm 0.1b	21.4 \pm 0.4a	23.1 \pm 0.4b
3	5.5 \pm 0.1a	5.4 \pm 0.1a	16.2 \pm 0.2a	17.9 \pm 0.2b
4	5.8 \pm 0.2a	4.9 \pm 0.2b	19.0 \pm 0.1a	20.0 \pm 0.1b
5	12.3 \pm 0.6a	11.1 \pm 0.6a	15.1 \pm 0.1a	16.4 \pm 0.1b
Sub-total Nymphal	26.2 \pm 0.7a	23.5 \pm 0.7b	18.0 \pm 0.1a	19.3 \pm 0.1b

Means followed by the same letter within a row are not significantly different ($P > 0.05$, Bonferroni test).

^a Initial cohorts were comprised of second instar individuals, therefore development time values for the second instar represent a mean of partial life-stage estimates. All other instar development times are based on total life stage duration.

STEPHANITIS PYRIOIDES SURVIVAL IN THE PRESENCE AND ABSENCE OF PREDATORS

In the predation trials, significant differences in mean temperature occurred between northern and southern exposure habitats for all examined instars and the adult stage (Table 3). Statistical values for differences in mean thermal environments for each stage included the: second instar ($F = 23.24$; $df = 1, 35.1$; $P < 0.0001$), fourth instar ($F = 40.27$; $df = 1, 4$; $P = 0.032$), fifth instar ($F = 38.45$; $df = 1, 8.01$; $P < 0.0001$), and adults ($F = 17.16$; $df = 1, 30.5$; $P < 0.0001$). Temperature ranges in the northern and southern exposures, respectively, during predation trials were as follows: second instar (25.0°C, 30.7°C), fourth instar (26.3°C, 29.5°C), fifth instar (27.7°C, 34.2°C), and adults (20.4°C, 27.8°C).

Stephanitis pyrioides survivorship in predator absent treatments across exposures was relatively high, and generally increased as life stage progressed (Table 3). In the predator present treatments, habitat exposure (varied thermal habitat) influenced survival in only one of the four life stages tested. An exposure by predation interaction occurred for the fourth instar ($F = 12.00$; $df = 1, 40$; $P = 0.0013$). Fourth instar *S. pyrioides* attained 21% survival in the northern exposure and 36% survival in the southern exposure environment when a predator was present (Table 3). For second instars ($F < 0.01$; $df = 1, 40$; $P = 0.9529$), fifth instars ($F = 0.09$; $df = 1, 40$; $P = 0.7663$), and adults ($F = 1.14$; $df = 2, 40$; $P = 0.3300$), there were no significant interactive effects of exposure on prey survival. For the second ($F = 290.78$; $df = 1, 40$; $P < 0.0001$) and fifth instars ($F = 173.29$; $df = 1, 40$; $P < 0.0001$), the presence of a predator significantly decreased survival compared to predator absent treatments. However, predators did not significantly reduce adult survival ($F = 4.04$; $df = 1, 40$; $P = 0.0512$) relative to predator

absent treatments (Table 3). Comparisons between stages were not examined, as life-stage survival experiments coincided with each *S. pyrioides* life-stage appearing in the source population, and therefore each life stage examined was not present in every replicate (incomplete factorial). However, there was a strong general trend that for each successive life stage, *S. pyrioides* survival increased in predator treatments regardless of exposure (Table 3). Survival of fifth instar nymphs and adult *S. pyrioides* was approximately 2 – 3 times greater than that of second and fourth instar nymphs.

***STEPHANITIS PYRIOIDES* FECUNDITY IN THE ABSENCE OF PREDATORS**

Fecundity trials were conducted during the period of the *S. pyrioides* developmental trials; therefore temperature differentials between environments were the same. *Stephanitis pyrioides* oviposition rates did not differ between habitat exposures ($F = 0.01$; $df = 1, 5$; $P = 0.9420$) (Table 4).

Table 3. Mean \pm SE survival of inclusion caged *S. pyraoides* cohorts with and without predators on 'Delaware Valley White' azaleas, and associated thermal environments (mean \pm SE) in northern and southern exposures of field plots^a

Life Stage (instar)	Predator Absent		Predator Present		Temperature, °C	
	Northern	Southern	Northern	Southern	Northern	Southern
Nymphal						
(2)	16.7 \pm 1.0a	16.5 \pm 1.0a	5.0 \pm 1.0b	5.0 \pm 1.0b	19.5 \pm 0.2a	20.8 \pm 0.2b
(4)	16.8 \pm 0.6a	15.9 \pm 0.6a	4.1 \pm 0.6b	7.1 \pm 0.6c	14.4 \pm 0.2a	15.4 \pm 0.2b
(5)	18.2 \pm 1.0a	17.7 \pm 1.0a	12.2 \pm 1.0b	12.0 \pm 1.0b	15.0 \pm 0.2a	16.7 \pm 0.2b
Adult	17.3 \pm 0.5a	17.8 \pm 0.5a	16.6 \pm 0.5a	17.4 \pm 0.5a	16.5 \pm 0.2a	17.8 \pm 0.2b

Means followed by the same letter within a row for predation treatments or temperatures are not significantly different ($P > 0.05$, Bonferroni test).

^a Initial cohort size for each life stage was 20 individuals.

Table 4. Mean \pm SE fecundity of *S. pyrioides* on 'Delaware Valley White' azaleas with natural enemies excluded in northern and southern exposure field plots

Time Interval	Exposure ^a	
	Northern	Southern
1	8.5 \pm 1.3a	9.3 \pm 1.3a
2	6.0 \pm 0.7a	5.9 \pm 0.7a
3	5.7 \pm 0.9a	6.6 \pm 0.9a
4	11.9 \pm 2.1a	11.7 \pm 2.1a
5	14.7 \pm 1.3a	13.8 \pm 1.3a
Total Fecundity	9.4 \pm 1.0a	9.5 \pm 1.0a

Means followed by the same letter within a row are not significantly different ($P > 0.05$, Bonferroni test).

^aInitial cohorts were comprised of two female and two male *Stephanitis pyrioides* adults, fecundity estimates are the mean number of eggs per female per 8 d interval and mean number of eggs over 40 d.

DISCUSSION

Using the azalea / azalea lace bug system, this study examined *S. pyrioides* development and survival under varying light exposure / temperature habitats while controlling for differences in vegetational and structural complexity, predator abundance, and host plant quality. This study found that northern exposure habitats were cooler than southern exposure habitats and that *S. pyrioides* developed slower in the cooler habitat. However, differences in temperature, in the absence of predators, did not affect *S. pyrioides* survival. In the presence of predators, *S. pyrioides* survival was lower for all life stages examined, except adults. Moreover, predation of *S. pyrioides* by *C. carnea* was greater only for fourth instars in warmer, southern exposure habitats compared to cooler, northern exposure habitats. Exposure / temperature differences did not influence predation of second or fifth instar, or adult *S. pyrioides*.

In accord with Shrewsbury (1996), this study found temperature differences between environments differing in levels of shade. Shrewsbury (1996) found structurally complex urban landscapes, which contained vegetation in an overstory layer, $\cong 2.5^{\circ}\text{C}$ cooler than landscapes with simple structural complexity, and no overstory layer. This study found a difference of 1.4°C between northern and southern exposures, where shade effects lasted for $\cong 8$ h during morning periods in northern exposure habitats.

Stephanitis pyrioides development was delayed in cooler, northern habitats relative to warmer, southern habitats. This finding supports previous field studies that identified slower *S. pyrioides* development in cooler, complex landscapes (Shrewsbury 1996) as well as laboratory studies that strictly examined the influence of temperature on development (Neal and Douglass 1988, Braman et al. 1992, Lepping Chapter 1).

Differences in host-plant quality between azalea in northern and southern exposures may have influenced differences in *S. pyrioides* development. Trumbule and Denno (1995) found differences in *S. pyrioides* development when reared on shade grown and sun grown azalea. Other studies have identified differences in azalea cultivar susceptibility or resistance to *S. pyrioides* based on host plant measures such as leaf water content, leaf pubescence, and leaf composition (Schultz 1993, Balsdon et al. 1995, Wang et al. 1998). These studies have found differences in *S. pyrioides* performance across azalea with varying host-plant characteristics, although results are mixed. For example, Wang et al. (1998) identified susceptible azalea cultivars based on factors such as oviposition rate, percent emergence from the egg, feeding damage, and nymphal development. However, they also found differences in leaf water content and leaf pubescence across azalea cultivars, but neither was correlated with *S. pyrioides* performance or host-plant resistance. Moreover, Shrewsbury (1996) examined *S. pyrioides* performance on established azaleas in structurally simple and complex landscapes and found no differences in survival or fecundity between habitats.

The present study controls, in part, host-plant quality by testing a single cultivar grown under uniform conditions prior to treatment assignment. Although results of this study suggest that differences in host-plant quality did not exist, due to the nature of the exposure treatments, differences may have occurred. Nymphal survival in the absence of natural enemies, an indirect measure of host plant quality, did not differ between warmer southern and cooler northern exposures. Furthermore, in the present study, an overall difference of 1.4°C between thermal habitats resulted in an approximate 3 d developmental lag for nymphal populations in the cooler habitat. These differences in

nymphal development between cool and warm environments are consistent with controlled temperature studies for *S. pyrioides* (Lepping Chapter 1) which found an approximate 7 d developmental lag for each 3°C decrease in environmental temperature (range 18 – 24 °C). That is, for every $\cong 1^\circ\text{C}$ decrease in mean environmental temperature, total *S. pyrioides* nymphal development may be expected to extend approximate 2 days. If laboratory and field findings had been grossly inconsistent, then delays in nymphal development due to factors such as host plant quality may be of greater concern. These findings suggest that differences in development are not related to host-plant quality, but differences in temperature between disparate exposure environments.

The finding of no difference in *S. pyrioides* fecundity between northern and southern exposures also suggests that there was no host-plant quality difference, as well as no severe reproductive penalties associated with either light exposure / thermal habitat. Similarly, Shrewsbury (1996) found no difference in fecundity of *S. pyrioides* on established azalea in simple and complex habitats on established azalea. Moreover, Kintz and Alverson (1999) found no difference in *S. pyrioides* fecundity on azalea in shaded and non-shaded nursery environments. Conversely, related lace bug species as well as non-tingid herbivore species have been found to deposit more eggs in exposed or warmer environments (Shreeve 1986, Cappuccino and Root 1992).

In this study, introduction of *C. carnea* into the study system reduced *S. pyrioides* survival for all examined nymphal instars, regardless of the exposure / thermal environment. Interestingly, predator introduction did not reduce adult *S. pyrioides* survival compared to predator absent treatments, suggesting adult *S. pyrioides* are not susceptible to predation by second instar *C. carnea*. These results support those found by

Lepping (Chapter 1), where laboratory studies found that adult *S. pyrioides* were less vulnerable to predation than nymphs.

Interestingly in this study, there was little overall difference in predation of *S. pyrioides* by *C. carnea* between cooler, northern exposure habitats and warmer, southern exposure habitats. Of the life stages examined, predation only differed for fourth instar *S. pyrioides*, where there was greater predation in the cooler, northern exposure habitat. This finding is counter to results from a previous laboratory study (Lepping Chapter 1) which found overall greater predation of *S. pyrioides* in warmer environments. The discrepancy between laboratory and field studies may have been due to temporary shading effects that allowed late-day sun exposure and elevated temperatures in northern exposure habitats, as suggested by the temperature ranges reported herein. In northern exposure habitats, lower mean temperatures may result in slower *S. pyrioides* growth, which may in turn create a wider window of vulnerability on a time scale relative to nymphal development. However, in short-term predation trials, late-day sun exposure may have raised temperatures to levels that allowed predators a thermal-mediated window of opportunity, thereby equalizing predation across exposure habitats. Conversely, in laboratory predation studies, where temperature differences influenced predation levels, environmental temperatures were held constant for the duration of study. Alternatively, significant temperature differences for field survival trials may not have been biologically significant. The mean thermal environments created by differential exposures may be classified in similar biologically active ranges for this predator – prey interaction. Laboratory studies support this hypothesis (Lepping Chapter 1). In laboratory studies, *S. pyrioides* mortality due to *C. carnea* predation increased

when temperature increased from 18°C to 21°C, but predation did not differ between the 21°C and 24°C levels (Lepping Chapter 1). Other controlled temperature studies of predator – prey interactions have found consistent differences in mortality between temperature treatment levels, although temperature treatment level spacing varies greatly (Geden and Axtell 1988, Gillespie et al. 1999, Ba M’Hamed and Chemseddine 2001, Roy et al. 2002). Smaller temperature treatment spacing may be required to determine if there are temperature ranges or thresholds for biologically distinct predator – prey interactions.

By decoupling the variables of habitat complexity, predator abundance, host-plant quality, and temperature, this study demonstrated slower herbivore growth in shaded, cooler habitats, as well as no general effect of thermal environment obtained in this field study on *S. pyrioides* fecundity, or survival in the presence or absence of predation. However, this study was not able to decouple the effects of light exposure and temperature. Independent of temperature effects, this study supported previous findings of life-stage specific vulnerabilities for *S. pyrioides* where the presence of predators reduced nymphal *S. pyrioides* survival compared to absence of predation, except for adult *S. pyrioides*, for which predator presence or absence had no effect. These results suggest that slowed or delayed development of vulnerable *S. pyrioides* life stages may result in longer periods of vulnerability to predation. Longer periods of development / vulnerability in cooler habitats may translate into greater predation. Conversely, *S. pyrioides* that reach less vulnerable life stages faster, due to warmer thermal environments, may incur less overall predation. These results concur with those of Shrewsbury (1996). Shrewsbury (1996) found structurally complex urban landscapes

were cooler and supported a greater abundance of generalist predators than warmer, structurally simple landscapes. The combination of slower *S. pyrioides* development and greater natural enemy abundance in cooler environments may partially explain the refractory nature of structurally complex habitats to lace bug outbreaks. Greater abundance of *S. pyrioides* in sunny, exposed habitats may then be partially due to *S. pyrioides* exploitation of a thermal refuge. *Stephanitis pyrioides* populations in warmer, predator-sparse habitats may attain a degree of enemy-free space through a temperature-mediated mechanism dependent upon both spatial and temporal habitat characteristics (Damman 1987, Murdoch et al. 1989, Denno et al. 1990, Berdegue et al. 1996).

The findings of this work have direct implications for landscape pest management. This study examined the effects of thermal environmental variation, through the effect of shading, on pest development and susceptibility to predation. The developmental data for *S. pyrioides* allows for estimation of life-stage appearance, and therefore may aid in pest management decision making oriented to target pests in vulnerable stages. Pest managers identifying vulnerable *S. pyrioides* life stages may then estimate periods that biological control tactics may be most efficacious, as well as periods that alternative controls may be necessary. In nursery production systems, pest-managers may choose to partly shade azalea to simulate more natural azalea habitats, thereby potentially increasing the window of vulnerability of *S. pyrioides* populations for predators before action thresholds are exceeded. This work underscores the necessity for landscape pest monitoring, as the success of an Integrated Pest Management (IPM) program including conservation or augmentative biological control is dependent on targeting key pests in vulnerable stages (Raupp 1985, Raupp et al. 1992).

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