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Research

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Development and Survival of *Lygus hesperus* (Hemiptera: Miridae) Nymphs Under Constant and Variable Temperatures

Dale W. Spurgeon[1] **and Colin S. Brent**

Pest Management and Biocontrol Research Unit, USDA, ARS, ALARC, 21881 N Cardon Lane, Maricopa, AZ 85138, and [1]Corresponding author, e-mail: dale.spurgeon@ars.usda.gov

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ABSTRACT

Thermal environments of the arid western United States are often harsh compared with the ranges of temperatures favorable for development and survival of crop insect pests. In cotton [*Gossypium* spp. (Malvales: Malvaceae)], new irrigation practices such as deficit irrigation may impact populations of pest and beneficial arthropods by temporarily altering temperature profiles within the plant canopy. Most information regarding the temperature-dependent development and survival of an important cotton pest, the western tarnished plant bug (*Lygus hesperus* Knight), is derived from constant temperature studies. We examined the development and survival of *L. hesperus* nymphs under constant (±0.2°C) and variable (±8°C) temperature regimes at daily mean temperatures of 15, 22, and 29°C. Under the low temperature (15°C), stadium lengths and duration of the nymphal stage were shorter when temperatures were variable compared with a constant temperature. No differences in development times were observed between regimes at the medium temperature (22°C). Except for the first stadium, development times under the high variable temperature regime were longer compared with the high constant regime (29°C). Nymph survival was unaffected by temperature regime except at the lowest temperature, where daily thermal fluctuations substantially improved survival compared with the constant conditions. These results suggest that temporarily increased crop canopy temperatures caused by altered irrigation schemes are unlikely to substantially reduce the growth of *L. hesperus* populations. However, enhanced nymphal development and survival under low variable temperatures likely contribute to the survival of overwintering *L. hesperus* in the absence of acute, low-temperature mortality.

Key words: temperature, development, survival

Thermal environments of the arid and semiarid western United States are often harsh, with summertime air temperatures frequently exceeding 40°C. However, temperature profiles within plant canopies typically provide a range of thermal environments that are more moderate compared with air temperatures because of transpiration during the day or radiant cooling at night (Rosenberg 1974). The capacity for canopy cooling during the day is strongly influenced by water availability (Jackson et al. 1981, González-Dugo et al. 2006, Padhi et al. 2012). The increasingly limited availability of water for crop irrigation in the western United States has prompted efforts to develop alternative irrigation methods such as deficit irrigation (González-Dugo et al. 2006, Mahan et al. 2012). These methods, if adopted, will periodically alter the micrometeorology of crop canopies, and thereby could impact populations of pest and beneficial insects. Among the potentially impacted pest species is the western tarnished plant bug, *Lygus hesperus* Knight, which is the most important pest of cotton [*Gossypium* spp., (Malvales: Malvaceae)] in Arizona (Asiimwe et al. 2014).

Several studies have examined the influences of irrigation regime on population levels of pest and beneficial insects in cotton of the arid Southwest, including the impacts on *L. hesperus* (Leigh et al. 1970; Flint et al. 1994, 1996; Asiimwe et al. 2014). Leigh et al. (1970) and Flint et al. (1994, 1996) noted a marked increase in *L. hesperus* population levels associated with frequent irrigation. Asiimwe et al. (2014) reported a reduction in the numbers of *L. hesperus* nymphs in response to limited irrigation in 1 yr of study, but not during the second study year. Although higher numbers of *L. hesperus* were generally associated with more frequent irrigation, the response to irrigation was also influenced by the impacts of insecticide applications on resident predators (Asiimwe et al. 2014). In contrast, Munk and Goodell (2002) reported that populations of *L. hesperus* nymphs were suppressed by drought conditions, whereas responses of adults was limited to a population increase only in the plots receiving the highest levels of irrigation. Although these reports generally indicate population responses by *L. hesperus* to irrigation regime, they provide few insights into the mechanisms governing those responses. It is particularly relevant to management efforts to understand whether observed population responses might be caused by the temperature dependence of development or mortality, or by some other factor such as host-preferences of the mobile adults.

Several studies document the influences of constant temperatures on development and mortality of *L. hesperus* eggs and nymphs (Champlain and Butler 1967; Butler and Wardecker 1971; Cooper and Spurgeon 2012, 2013) and on the reproductive development of adults (Spurgeon and Cooper 2012). However, Hagstrum and Milliken (1991) reported that for many species of insects, development rates at constant temperatures poorly reflect development under variable temperatures, especially when the mean daily temperature is high. Champlain and Butler (1967) reported that development times of *L. hesperus* eggs were similar under constant and variable temperatures, and Butler and Watson (1974) found that development times of all stages of *L. hesperus* under constant temperatures were predictive of development times under variable temperatures. Brent and Spurgeon (2019) examined oviposition under different constant and variable (±8°C) temperature regimes. They found that temperature influenced the rate of oviposition and longevity of adult females, but lifetime oviposition was unaffected by temperature regime. In contrast, Spurgeon and Brent (2016) found that egg hatch and survival were enhanced by variable temperatures compared with a low constant temperature (15°C), whereas the opposite effect of variable temperatures was observed when the mean daily temperature was high (29°C). Herein, we examine the influences of temperature and temperature regime (constant, variable) on development and survival of *L. hesperus* nymphs.

Materials and Methods

Newly hatched nymphs were obtained from eggs deposited by adult *L. hesperus* that were collected from fields of alfalfa [*Medicago sativa* L. (Fabales: Fabaceae)] near Maricopa, AZ. The field collected adults were held in 0.03-m^3 screened cages provisioned with shredded paper, a water saturated cotton pad, raw seeds of sunflower [*Helianthus annuus* L. (Asterales: Asteraceae)], and pods of green bean [*Phaseolus vulgaris* L. (Fabales: Fabaceae)] that served as food and oviposition substrate. The parent colony was maintained at 27 ± 1°C with a 14:10 (L:D) h photoperiod. Bean pods containing eggs that were oviposited over a 6–8 h period were held at 26.7 ± 0.5°C with a photoperiod of 14:10 (L:D) h until hatch.

Upon hatching, thirty first instars were assigned to each of six I30-BLL environmental chambers (Percival Scientific, Perry, IA) set at a photoperiod of 14:10 (L:D) h. Each chamber was set to one of six combinations of mean daily temperature (15, 22, or 29°C) and temperature regime (constant, variable). These treatment combinations were identical to those used by Spurgeon and Brent (2016) and Brent and Spurgeon (2019). The high variable temperature regime was intended to represent canopy temperatures in moderately drought stressed cotton (Wanjura et al. 2004, Carmo-Silva et al. 2012, Mahan et al. 2012, Sui et al. 2012). Briefly, variable temperature regimes featured an amplitude of ±8°C from the daily mean temperature. In each variable treatment, the temperature was increased linearly from the daily low at 0600 h to the daily high at 1600 h, where it was maintained until 2000 h. At 2000 h, the temperature began to decrease linearly until it reached the daily low at 0200 h, where it was held constant until 0600 h. These temperature regimes were obtained using a temperature ramping feature of the chambers (Percival Scientific). Temperatures in all chambers were monitored at least three times weekly using temperature loggers (U10-003, Onset Computer, Bourne, MA). Temperature offsets of the chambers were adjusted as needed to maintain the desired temperature treatments. Temperature records indicated both constant and variable regimes were controlled to within 0.2°C of the desired mean daily temperature.

At hatching, each nymph was individually confined within an 18-ml plastic vial (Thornton Plastics, Salt Lake City, UT) closed with a screened, snap-cap lid. Each vial was provisioned with a section of green bean pod with cut ends sealed with paraffin. Bean sections were replaced three times weekly. Nymphs were examined at least once daily to detect molting, mortality, and gender of the emerging adult.

The experiment was conducted as a randomized complete block where the two experimental repetitions formed the blocks. Within each block, newly hatched nymphs were randomly assigned to each treatment combination as they became available, which sometimes occurred over 2 d. Each block was represented by a distinct collection of parent adults, and for each treatment combination, the experimental unit was the cohort of 30 nymphs.

Stadium duration of each instar, and total nymphal development time, were compared among the temperature treatments using conditional models estimated by the Laplace method (PROC GLIMMIX, SAS Institute 2012). The sole exception was duration of the third stadium, which was analyzed using a generalized estimating equation (GEE) approach to achieve convergence. All analyses fit the responses to a Gamma (time-to-event) distribution, and the GEE analysis used the Kenward-Roger degree of freedom adjustment. Each model included fixed effects of temperature, regime, and their interaction, and random effects of block, and the temperature by regime by block interaction to serve as the error term for testing the fixed effects. Cooper and Spurgeon (2012) found that the development times of male and female *L. hesperus* were indistinguishable over a wide range of temperatures, so insect gender was not included as a model effect. Where interactions were judged to be nonnegligible, simple effects were examined using the SLICE and SLICEDIFF options of the LSMEANS statement. Experiment-wise type-I error rates for multiple comparisons were maintained at 0.05 using the SIMULATE option as the multiplicity adjustment.

Nymphal survival was examined using a GEE model with a binomial distribution and the Kenward-Roger degree of freedom adjustment. Fixed and random model effects were exactly the same as in the analyses of stadium duration. Because the number of nymphs that died during a given stadium within a temperature by regime combination was usually low (1–4), only mortality over the entire nymphal stage was examined.

Results

In each examination of the influences of temperature and temperature regime on the durations of nymphal stadia or the entire nymphal stage, the temperature by regime interaction was significant (Table 1). At the lowest mean daily temperature (15°C), each stadium duration was shortened in response to variable temperatures compared with the constant temperature treatment (Table 2, Fig. 1a–f). At the highest daily mean temperature (29°C), the opposite trend was observed, with development occurring more rapidly in the constant temperature regime compared with the variable regime (Table 2, Fig. 1b–f). The sole exception at the highest temperature

Table 1. Fixed effect tests of the influence of daily mean temperature (15, 22, or 29°C) and temperature regime (constant [±0.2°C] or variable [±8°C]) on development time of *L. hesperus* instars and of the nymphal stage

	Temperature			Regime			Temperature by regime		
Instar	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*
1	477.91	2, 5	<0.001	5.30	1, 5	0.070	9.98	2, 5	0.018
2	920.75	2, 5	<0.001	5.44	1, 5	0.067	42.45	2, 5	<0.001
3	1064.79	2, 5.40	<0.001	9.22	1, 5.48	0.026	31.28	2, 5.41	0.001
4	1171.23	2, 5	<0.001	4.40	1, 5	0.090	23.82	2, 5	0.003
5	2186.11	2, 5	<0.001	39.68	1, 5	0.002	96.06	2, 5	<0.001
Nymph	5372.34	2, 5	<0.001	50.32	1, 5	<0.001	164.55	2, 5	<0.001

Analyses used a conditional model with a Gamma distribution except for tests of the third instar, which used a marginal, generalized estimating equation model with a Gamma distribution and the Kenward-Roger degrees of freedom correction.

Table 2. Simple effect tests of the influences of temperature regime (constant [±0.2°C], variable [±8°C]) on *L. hesperus* stadium lengths and duration of the nymphal stage at three temperatures with a photoperiod of 14:10 (L:D) h

Temperature	Stadium/stage	*F*	df	*P*
15	1	22.74	1, 5	0.005
	2	54.66	1, 5	<0.001
	3	53.82	1, 7.185	<0.001
	4	41.82	1, 5	0.001
	5	176.56	1, 5	<0.001
	Nymph	288.39	1, 5	<0.001
22	1	0.18	1, 5	0.690
	2	2.31	1, 5	0.189
	3	1.02	1, 4.704	0.362
	4	0.32	1, 5	0.596
	5	6.46	1, 5	0.052
	Nymph	4.35	1, 5	0.091
29	1	1.74	1, 5	0.244
	2	30.54	1, 5	0.003
	3	13.46	1, 4.738	0.016
	4	7.56	1, 5	0.040
	5	35.41	1, 5	0.002
	Nymph	66.82	1, 5	<0.001

Analyses used a conditional model with a Gamma distribution except for tests of the third stadium, which used a marginal, generalized estimating equation model with a Gamma distribution and the Kenward-Roger degrees of freedom correction.

was for duration of the first stadium, which was numerically shorter under constant temperatures but not significantly different from the stadium duration under the variable regime (Table 2, Fig. 1a). At the moderate temperature (22°C), no differences in development time were demonstrated between constant and variable temperature regimes for any instar or for the nymphal stage (Table 2, Fig. 1a–f). Overall, the variable temperature regime produced development times that were 70–77% of those observed for the constant temperature regime at a daily mean temperature of 15°C, and 108–124% of those for the constant regime at a mean temperature of 29°C.

Simple effect tests comparing among mean daily temperatures within temperature regimes uniformly indicated the temperature dependence of development (Table 3). Multiple comparisons among temperatures indicated a significant decrease in stadium length, and in duration of the nymphal stage, with each increment of temperature increase irrespective of whether the temperature regime was constant or variable (Fig. 1).

Analysis of nymphal survival also indicated a significant temperature by regime interaction ($F = 5.93$, df = 2, 5.003; $P = 0.048$). Simple effect tests comparing mortality between temperature regimes within temperatures indicated a significant difference only at the lowest mean daily temperature (15°C; $F = 16.93$; df = 1, 5.002; $P = 0.009$; Fig. 2). Although the data suggested subtle numerical differences between regimes at the other temperatures, presence of such trends were not supported by the simple effect tests (22°C, $F = 0.03$; df = 1, 5.001; $P = 0.875$; 29°C, $F = 0.68$; df = 1, 5.004; $P = 0.446$; Fig. 2). The simple effects tests comparing nymphal mortality among temperatures within the variable temperature regime indicated no differences ($F = 1.88$; df = 2, 5.002; $P = 0.246$; Fig. 2). Those results contrasted with the simple effect tests for the constant temperature regime, where a difference among temperatures in nymphal mortality was clear ($F = 25.90$; df = 2, 5.001; $P = 0.002$). Multiple comparisons among temperatures within the constant regime indicated substantially greater mortality for nymphs under the lowest temperature (15°C) compared with either 22 or 29°C (Fig. 2).

Discussion

Hagstrum and Milliken (1991) reported that where differences in development time were observed between constant and variable temperature regimes, the variable regimes tended to reflect the effects of the higher temperature portions of their temperature profiles. That is, at lower temperatures development tended to occur more rapidly under variable regimes compared with constant temperatures, whereas the opposite was observed for higher temperatures. Their report is entirely consistent with our observations of *L. hesperus* nymphal development. In addition, our observations of the influence of variable temperatures on nymphal development are similar to the effects reported for *L. hesperus* eggs (Spurgeon and Brent 2016). Our results are not consistent with previous reports of little or no difference in *L. hesperus* development times between constant and variable temperatures (Champlain and Butler 1967, Butler and Watson 1974).

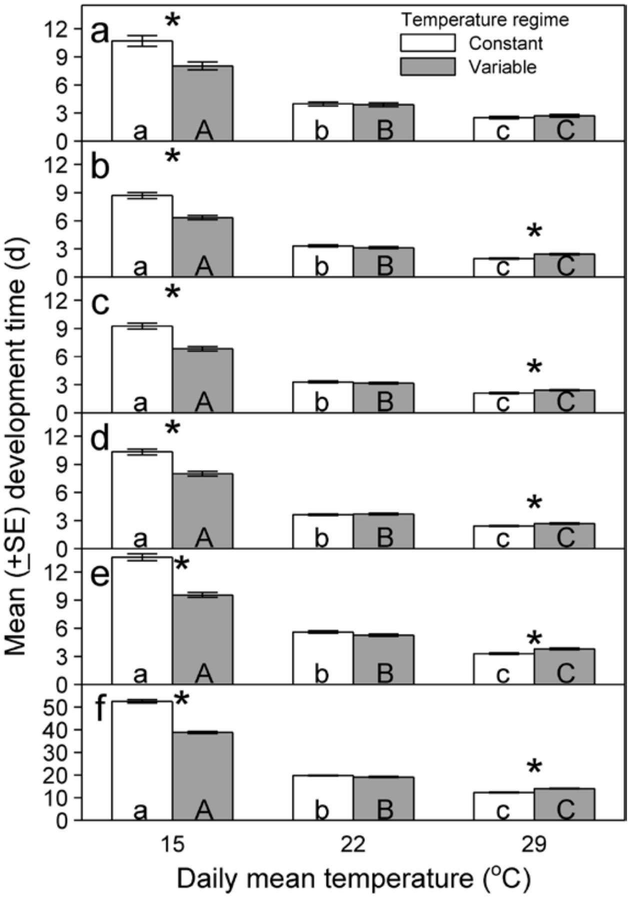

Fig. 1. Mean (±SE) stadium lengths for *L. hesperus* first (a), second (b), third (c), fourth (d), and fifth instars (e), and total nymph development time (f) under selected constant (±0.2°C) and variable (±8°C) temperature regimes with a photoperiod of 14:10 (L:D) h. Paired bars within an instar marked by an asterisk (*) indicate a significant difference ($\alpha < 0.05$) between temperature regimes. Bars within an instar marked by the same lowercase (constant temperature) or uppercase letters (variable temperature) are not significantly different at experiment-wise $\alpha = 0.05$.

Of the several studies examining *L. hesperus* population responses to irrigation in cotton (Flint et al. 1994, 1996; Leigh et al. 1970; Munk and Goodell (2002) , only Asiimwe et al. (2014) measured canopy temperatures. However, the irrigation regimes used by Asiimwe et al. (2014) were not sufficiently different to induce corresponding differences in canopy temperatures. Therefore, it is not possible to infer the potential role of the thermal environment on the results of these previous studies. Although our results indicate a significant increase in *L. hesperus* nymphal development time at high variable temperatures compared with a constant temperature, the differences we observed were relatively small (10–15%) and would likely not produce a strong population response. These differences were similar in magnitude to the effects on egg development of high variable temperatures reported by Spurgeon and Brent (2016). We anticipated a marked influence of the high variable temperature regime on nymphal survival because Cooper and Spurgeon (2012) noted the high-temperature inhibition of nymphal development at temperatures above ≈31°C, low survival to adulthood at a constant 35°C, and complete mortality at a constant 37.8°C. Therefore, during our study the deleterious effects of periodic temperatures >31°C were apparently moderated by the intervening periods of lower temperature. Considering also the lack of influence by the high temperature regime on lifetime oviposition (Brent and Spurgeon 2019), our results suggest the population responses previously observed in irrigation studies in cotton were more likely the product of host preferences exhibited by the mobile adults, or altered relationships between *L. hesperus* and its natural enemy complex, rather than direct effects of the thermal environment on *L. hesperus* reproduction or survival.

In contrast to the modest influence on nymphal development and survival of the variable temperature regime centered on 29°C, the more substantial influence at the lowest temperature (15°C) may have important implications for *L. hesperus* overwintering. Cooper and Spurgeon (2012) reported greatly prolonged development, and high mortality, of nymphs exposed to constant 10° or 12.8°C. Although nymphal mortality observed at constant 15°C in our study was not excessive, it was more than twice that observed under the corresponding variable temperature regime.

Table 3. Simple effect tests of the influences of temperature (15, 22, or 29°C) on *Lygus hesperus* stadium lengths and duration of the nymphal stage within constant (±0.2°C) or variable (±8°C) temperature regimes with a photoperiod of 14:10 (L:D) h

Regime	Stadium/stage	*F*	df	*P*
Constant	1	306.59	2, 5	<0.001
	2	633.81	2, 5	<0.001
	3	686.03	2, 5.702	<0.001
	4	727.64	2, 5	<0.001
	5	1503.88	2, 5	<0.001
	Nymph	3488.06	2, 5	<0.001
Variable	1	178.63	2, 5	<0.001
	2	308.57	2, 5	<0.001
	3	390.50	2, 5.093	<0.001
	4	456.07	2, 5	<0.001
	5	728.46	2, 5	<0.001
	Nymph	1949.86	2, 5	<0.001

Analyses used a conditional model with a Gamma distribution except for tests of the third stadium, which used a marginal, generalized estimating equation model with a Gamma distribution and the Kenward-Roger degrees of freedom correction.

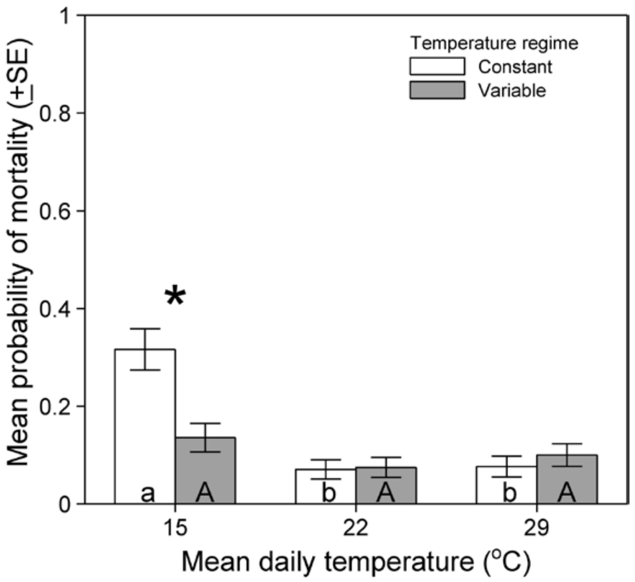

Fig. 2. Mean (±SE) probability of mortality for *L. hesperus* nymphs under selected constant (±0.2°C) and variable (±8°C) temperature regimes with a photoperiod of 14:10 (L:D) h. Paired bars marked by an asterisk (*) indicate a significant difference ($\alpha < 0.05$) between temperature regimes. Bars marked by the same lowercase (constant temperature) or uppercase letters (variable temperature) are not significantly different at experiment-wise $\alpha = 0.05$.

Lygus hesperus are known to survive at least part of the noncropping season in a photoperiodically induced diapause of relatively short duration (Beards and Strong 1966, Leigh 1966, Strong et al. 1970). Although each of these reports indicate the adult diapause terminates in late fall or early winter, they differ in perspective regarding the mechanisms of overwintering after diapause termination. Beards and Strong (1966) suggested that nymphs in the field during late October and November do not enter diapause as adults, mid-winter populations are composed of ovipositing adults, and the late winter is passed in the egg stage. Leigh (1966) implied the postdiapause adults completed overwintering on 'an abundant supply of suitable host material'. Strong et al. (1970) suggested that spring populations resulted from eggs deposited during winter, but that only eggs laid after mid-February survived to hatch. However, Spurgeon and Brent (2015) observed that only a portion of the *L. hesperus* adult population enters diapause in central Arizona, and Spurgeon (2017) reported observing diapausing adults in March These observations, combined with the greatly extended longevity of reproductive adults at low temperatures (Cooper and Spurgeon 2015), prompted Spurgeon (2017) to suggest that where wintertime temperatures are mild, the overwintering population of *L. hesperus* likely includes overlapping generations of both reproductive and diapausing individuals. Finally, the results of Spurgeon and Brent (2016), indicating enhanced development and survival of eggs under variable low temperatures, compared with a constant low temperature, were similar to observations for nymphs from this study. These collective observations indicate that studies of *L. hesperus* eggs and nymphs under low but above-freezing constant temperatures have substantially overestimated development times and mortality, compared with development and mortality that occur under variable temperatures that better represent the thermal environment in the field. These findings seem to warrant additional investigation into the population dynamics and mechanisms of overwintering in southern populations of *L. hesperus*.

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