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Development, Survival, and Hatching Periodicity of *Lygus hesperus* (Hemiptera: Miridae) Eggs under Constant and Variable Temperatures[1]

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Abstract The microclimate within western cotton (*Gossypium* spp.) seems favorable for the western tarnished plant bug (*Lygus hesperus* Knight) (Hemiptera: Miridae), provided adequate soil moisture is available. Diminishing water supplies and increasing costs in the West will likely change irrigation practices and induce at least periodically unfavorable conditions for *L. hesperus*. Knowledge of *L. hesperus* thermal ecology has been limited to constant temperatures for which relevance to variable temperature environments is unknown. Eggs of *L. hesperus* were reared under low (mean = 15°C), medium (mean = 22°C), or high (mean = 29°C) constant (±<0.5°C) or diurnally fluctuating (±8°C) temperatures. Developmental time and survival were similar between constant and variable regimes at the medium temperature. In contrast, variable low temperatures hastened egg development and increased survival, whereas variable high temperatures delayed development and reduced survival compared with constant regimes. Within the studied temperature range, the relationship between temperature and egg developmental rate was linear for constant temperatures, but a quadratic term was needed to describe this relationship under variable temperatures. Under medium variable temperatures, egg hatch was disproportionately high during the warmest period of the day (1300–1900 h) compared with the constant regime. Differences between regimes were less pronounced at high temperatures, except for the conspicuous absence of hatch between 1300 and 1900 h in the variable regime when temperatures were always >32°C. These results indicate the limited utility of constant temperature data for understanding *L. hesperus* thermal ecology and provide baseline information to better plan and interpret applied studies of *L. hesperus* thermal ecology.

Key Words *Lygus hesperus*, western tarnished plant bug, thermoperiod, development

Improved management of the western tarnished plant bug, *Lygus hesperus* Knight (Hemiptera: Miridae), in cotton (*Gossypium* spp.) in Arizona (Ellsworth 1998) and the availability of reduced-risk insecticides (University of Arizona 2013) has diminished the pest status of this insect. The decline in economic importance increases the difficulty of efforts to achieve additional, incremental improvements in *Lygus* spp. management through conventional approaches. However, the current low-pesticide-use environment in Arizona cotton may provide opportunity for low-

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cost, ecologically based management tactics if *L. hesperus* physiological ecology is sufficiently understood.

The agricultural environment in much of Arizona is harsh, with air temperatures often exceeding levels that are lethal to pest and beneficial insects. Insect survival and reproduction in this environment are facilitated by favorable thermal conditions within crop canopies, in which temperatures are typically lower than that of the ambient air (Carmo-Silva et al. 2012, Sui et al. 2012). Maintenance of canopy temperatures at levels lower than ambient is dependent on the availability of soil moisture (González-Dugo et al. 2006, Jackson et al. 1981, Padhi et al. 2012). However, limited water availability in western production regions is prompting development of alternative irrigation strategies such as deficit irrigation (Mahan et al. 2012, Wanjura et al. 2004, Wen et al. 2013) along with research to better understand crop responses to heat and drought (Carmo-Silva et al. 2012, Pilon et al. 2014). Adoption of alternative irrigation strategies are likely to result in at least periodic within-canopy thermal environments that are unfavorable for insect development or survival. Whether these conditions can be exploited to better manage pests will depend on improved knowledge of insect thermal ecology, and possibly on an exploration of transcriptomic resources (Hull et al. 2013, 2014) for identification of environmentally sensitive targets for disruption.

Until recently, the relationship between temperature and development of *L. hesperus* eggs was characterized by linear regression models confined to relatively narrow temperature ranges (Butler and Wardecker 1971, Champlain and Butler 1967). Based on these limited data, Champlain and Butler (1967) reported that developmental rates of *L. hesperus* eggs under constant temperatures were similar to those observed under variable temperatures. Cooper and Spurgeon (2013) expanded the range of observed temperatures and described the temperature dependence of egg development through nonlinear functions (Schoolfield et al. 1981, Sharpe and DeMichele 1977) by using a program modified from Wagner et al. (1984). Those functions demonstrated both low- and high-temperature inhibition of *L. hesperus* egg development. The occurrence of temperature-dependent inhibition of development suggests development under constant temperatures should be dissimilar to development under variable temperatures that encompass the lower or upper thermal limits for development, as observed for numerous insects by Hagstrum and Milliken (1991). Therefore, investigation of *L. hesperus* egg development under variable temperature regimes would provide insight into the applicability of constant temperature results to ecologically meaningful, variable temperature environments.

Materials and Methods

Egg development and survival. Eggs were obtained from the F_1 or F_2 progeny of adult *L. hesperus* collected from alfalfa (*Medicago sativa* L.). The original field collections were made in November 2013, May 2014, and March 2015. Each collection included 400–500 adults maintained on green bean (*Phaseolus vulgaris* L.) pods and raw sunflower (*Helianthus annuus* L.) seeds at ~27°C, with a photoperiod of 14:10 (L:D) h, as described by Spurgeon and Brent (2015).

For each repetition of the experiment, a mixed sex group of 300–500 young adults (0–3 d old) was held in a collapsible cage (30.5 × 30.5 × 30.5 cm; BioQuip, Rancho Dominguez, CA) provisioned with shredded paper and a sheet of Hexcel (PN1, Hexcel, Pleasanton, CA) for refuge. Each cage contained a water source of saturated cotton in a Petri plate bottom and raw sunflower seeds in a Petri plate lid. The insects were fed fresh green bean pods three times weekly until the desired number of eggs was obtained.

When adults were ≥8 d old, females were individually aspirated from the rearing cage and placed in a clear sealable plastic bag. Because virgin females frequently oviposit, the ventral abdomen of each female was examined under a dissecting microscope for externally visible evidence of a spermatophore, indicating recent mating (Cooper 2012). Unmated females were returned to the rearing cage for collection on subsequent days until egg collection was complete. Each mated female was individually confined within an 18-ml plastic vial (Thornton Plastics, Salt Lake City, UT) closed with a screened snap-cap lid and a section of green bean pod as oviposition substrate. The cut ends of each bean section were sealed with melted paraffin to minimize desiccation and to prevent newly hatched nymphs from hiding within the bean. After a 6–8-h oviposition period, each bean section was examined for eggs that were identified by a number drawn on the bean pod with a permanent pen (Pigma Micron 005, Sakura Color Products of America, Hayward, CA). The numbers of eggs deposited varied considerably among females, and previous observations suggested greater variation in egg developmental time among eggs laid by different females than among eggs laid by a single female (W.R. Cooper, pers. comm.). Therefore, a maximum of five eggs were monitored for a given female. Bean sections containing eggs were returned to their respective vials and assigned to temperature treatments. Females laying eggs were held separately from the unmated adults to ensure the same females were not represented more than once. Egg collection continued until 50 eggs were obtained for each temperature treatment.

The study included three variable temperature treatments, each paired with a corresponding constant temperature treatment. The six temperature treatments were designated as follows: (1) low variable (7–23°C, mean = 15°C), (2) low constant (15°C), (3) medium variable (14–30°C, mean = 22°C), (4) medium constant (22°C), (5) high variable (21–37°C, mean = 29°C), and (6) high constant (29°C). The mean temperature and amplitude of the high variable treatment were selected based on reports of cotton canopy temperatures during moderate drought stress (Carmo-Silva et al. 2012, Mahan et al. 2012, Sui et al. 2012, Wanjura et al. 2004). Amplitudes of the medium variable and low variable regimes were the same as for the high variable regime because Hagstrum and Milliken (1991) reported both mean temperature and amplitude influenced insect developmental time. The mean temperature of the medium variable regime was selected so that the range of daily temperatures was contained within the portion of the developmental rate curve that is approximately linear (Cooper and Spurgeon 2013). The mean of the low variable regime was selected such that the daily low temperature was below the estimated lower thermal threshold for *L. hesperus* egg development (Cooper and Spurgeon 2013).

Each temperature treatment was assigned to an environmental chamber (I30BLL, Percival Scientific, Perry, IA). In each variable temperature regime, the

low temperature was maintained from 0200 h until the chamber lights were started (0600 h). The temperature was then linearly increased to the high temperature by 1600 h, where after it was maintained until the chamber lights were stopped (2000 h), and then decreased linearly to the low temperature by 0200 h. Thus, warming and high temperatures occurred during the 14-h photophase, whereas declining and low temperatures occurred during the 10-h scotophase. Variable and constant temperature treatments were monitored using portable temperature loggers (U10-003, Onset Computer, Bourne, MA), from which data were downloaded at least twice weekly. Temperature offsets on the environmental chambers were adjusted to ensure that low, high, and mean temperatures in the variable temperature regime and mean temperatures in the constant temperature regimes were maintained within ± 0.5°C of the desired setting.

In total, 50 eggs, originating from 11 to 15 adult females, were established in each temperature treatment for each repetition of the experiment. Numbered eggs were examined daily for hatch or mortality. After extension of the operculum (Cooper and Spurgeon 2012a), eggs were observed at least twice daily, with observations terminating in late afternoon or early evening. Egg hatch was signified by dislocation of the operculum and an empty chorion. In addition, the serosal cuticle was usually apparent. Egg mortality was indicated by collapse of the operculum or other evidence of desiccation after failure to hatch. At each observation, newly hatched first instars were removed to minimize the possibility of their predation on remaining eggs.

Because the number of environmental chambers was initially limiting, an incomplete block design was used. Each treatment was repeated three times in total within four repetitions (blocks) of the experiment. Egg developmental times (days) were examined using mixed-model, heterogeneous errors analysis of variance (PROC GLIMMIX, SAS Institute 2012). Fixed effects included temperature (daily mean), regime (constant, variable), and their interaction. Random effects included repetition of the experiment (block), ovipositing female, and the block $\times$ temperature $\times$ regime interaction, which was included as the error term for testing fixed effects. Because the temperature $\times$ regime interaction was significant, simple effects were examined for temperature within each regime, and regime within each temperature. Tests comparing developmental time among temperatures within each regime were adjusted for multiplicity by using the SIMULATE option of the LSMEANS statement.

The relationship between temperature and developmental rate for each regime was also described by mixed model regression with heterogeneous errors (PROC GLIMMIX). In these models, repetition of the experiment and the repetition $\times$ temperature interaction were included as random effects. The latter term served as the error term in the model. Therefore, although the developmental rate for each egg was included in the analyses, the estimated regression lines described developmental rate by using each group of eggs in each combination of temperature, regime, and block as the experimental unit (observation).

The probability of egg survival to hatch was examined using a conditional generalized mixed model with a binomial distribution. The Laplace method was used for computing the model (PROC GLIMMIX). Fixed effects included temperature, regime, and their interaction, and repetition of the experiment was a random effect. Because the temperature $\times$ regime interaction was significant,

simple effects of each factor were examined over levels of the other factor, as previously described.

Diel periodicity of egg hatch. During the investigation of egg developmental time, an observed diel periodicity of hatch was apparently associated with temperature regime. Therefore, a second experiment examined this periodicity. Eggs were obtained from adults of unknown age reared in the laboratory as previously described for three or fewer generations. In each repetition of the experiment, 12 bean pods were removed from the adult colony cage 18–24 h after the colony was serviced. Whole pods were used to eliminate the opportunity for hatching nymphs to hide within the pods. Three bean pods were randomly assigned to each of four temperature treatments: medium variable, medium constant, high variable, and high constant treatments from the developmental time experiment. The beans assigned to each treatment were confined together within a 3.7-liter plastic rearing bucket (12841A, Devore Packaging, San Clemente, CA) closed with a solid lid to prevent desiccation of the beans. Beginning 2–3 d after establishment of the treatments, buckets were examined daily, and condensation from the bucket sides and lids was removed by blotting.

Beginning on day 5 after oviposition for the high constant treatment, day 6 for the high variable treatment, and day 8 for both medium temperature treatments (1 d before anticipated first hatch), buckets were inspected for nymphs at 0700, 1300, and 1900 h. At each observation, newly hatched nymphs were counted and discarded. Inspections continued until 24 h after the last observed hatch. The experiment was conducted three times (blocks).

Differences in the periodicity of egg hatch between temperature regimes were examined separately for each temperature by using contingency tables. The analysis used the Cochran–Mantel–Haenszel test of general association (Q_{GMH}) stratified over repetition of the experiment (PROC FREQ, SAS Institute 2012). Because of slight shifts in the timing of first hatch among experimental repetitions and low numbers of nymphs in the earliest and latest time intervals, in each test the center nine time periods were analyzed. Although observed counts of hatched nymphs at each observation were analyzed, results are presented as the proportion of hatch per 6 h for improved clarity. This approach compensates for different sample sizes (numbers of hatched nymphs) among treatments and the unequal hatch periods (each observation at 0700 h represented a 12-h period, whereas other observation times represented 6-h periods).

Results

Egg development and survival. In the combined repetitions of the experiment, the total numbers of eggs hatching at each combination of temperature and regime ranged from 101 (constant, low temperature) to 145 (variable, medium temperature). Egg developmental time was influenced by both temperature ($F = 3111.31$; df $= 2, 6.85$; $P < 0.01$) and regime ($F = 74.45$; df $= 1, 6.41$; $P < 0.01$), but their interaction indicated the effects of regime varied among temperatures ($F = 111.33$; df $= 2, 5.54$; $P < 0.01$; Fig. 1). Examination of simple effects of regime within each

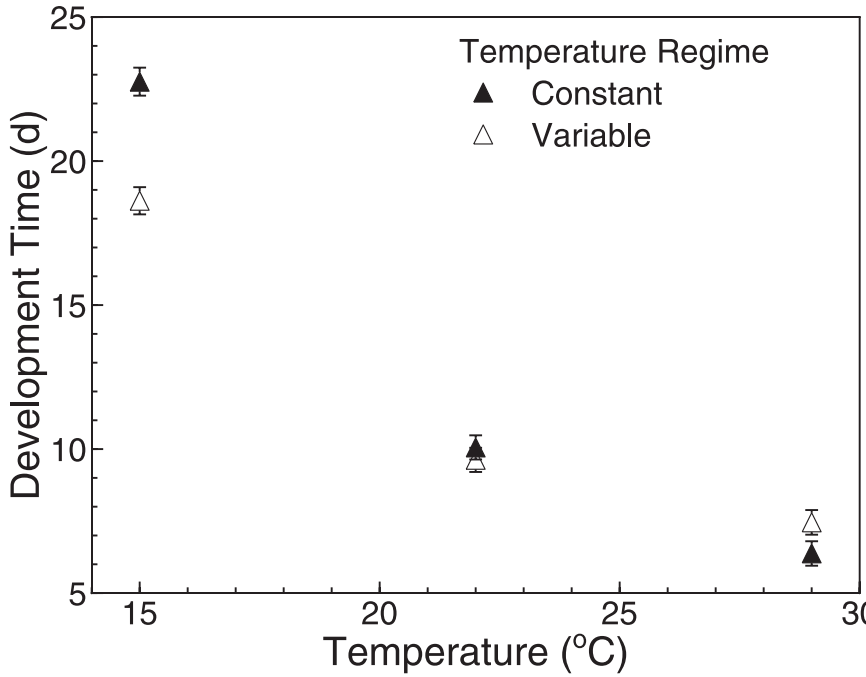

Fig. 1. Mean (±95% confidence limits) developmental times of *Lygus hesperus* eggs under constant (±<0.5°C) and variable (±8°C) temperature regimes.

temperature revealed that developmental time was longer for the variable temperature regime compared with the constant regime at the high temperature ($F = 28.00$; df = 1, 3.78; $P < 0.01$), whereas the opposite effect of regime occurred at the low temperature (F 214.93; df = 1, 13.75; $P < 0.01$). In contrast, no influence of regime was demonstrated at the medium temperature ($F = 4.40$; df = 1, 3.76; $P = 0.11$).

The relationship between developmental rate and constant temperature was approximately linear within the observed temperature range (15–29°C; Fig. 2). Both the intercept ($t = -35.60$, df = 4.79, $P < 0.01$) and slope ($t = 78.40$, df = 5.85, $P < 0.01$) were significant. Extrapolation of the regression line to intersection with the *x*-axis estimated the lower thermal threshold for egg development at 9.6°C. The relationship between developmental rate and mean daily temperatures of the variable regimes was curvilinear and required addition of a quadratic term to the model (Fig. 2). All three model terms were significant (intercept: $t = -9.84$, df = 3.22, $P < 0.01$; slope: $t = 12.46$, df = 3.33, $P < 0.01$; quadratic slope: $t = -7.68$, df = 3.54, $P < 0.01$). This polynomial regression estimated the lower threshold for egg development as 9.4°C.

Egg survival to hatch was high overall (83%), but some differences were demonstrated among combinations of temperature and regime. Although analyses indicated significance of the temperature effect ($F = 4.98$; df = 2, 9; $P = 0.04$), but

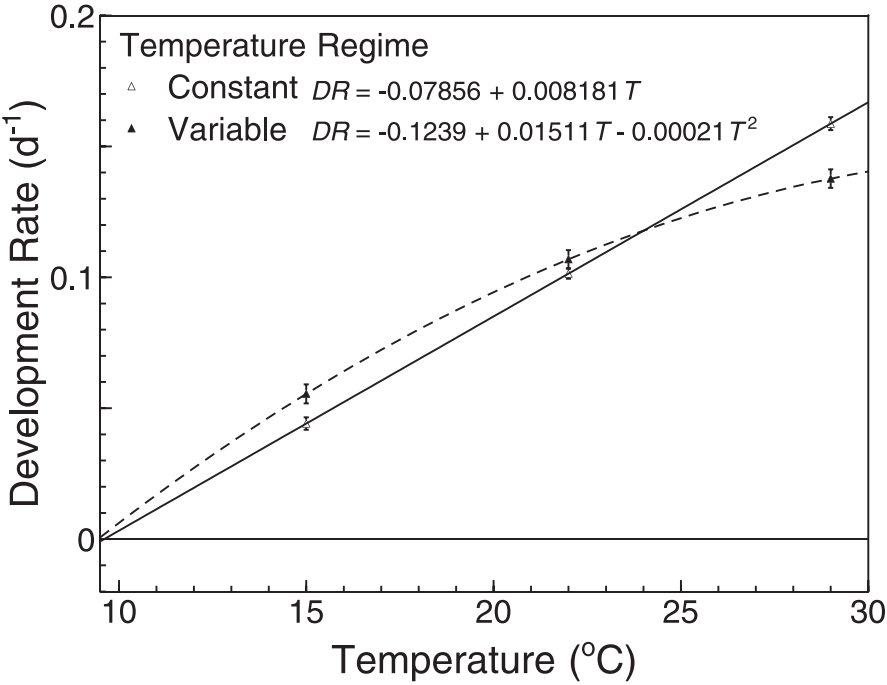

Fig. 2. Regression equations describing respective *Lygus hesperus* egg developmental rates under constant and variable temperature regimes. *DR* is developmental rate and *T* is temperature (°C). Error bars represent 95% confidence limits.

not the regime effect ($F = 1.84$; df = 1, 9; $P = 0.21$), their interaction indicated the effects of temperature were not consistent among regimes ($F = 10.57$; df = 2, 9; $P < 0.01$; Table 1). Examination of simple effects for regime within temperatures indicated egg survival under the variable regime was higher than under the constant regime for the low temperature treatment ($F = 7.83$; df = 1, 9; $P = 0.02$), but survival was higher for the constant regime compared with the variable regime for the high temperature treatment ($F = 9.67$; df = 1, 9; $P = 0.01$; Table 1). No difference in egg survival was demonstrated between regimes in the medium temperature treatment ($F = 4.26$; df = 1, 9; $P = 0.07$). Comparisons among temperatures within the constant regime indicated higher survival at the high temperature than at the low temperature ($t = -3.84$, df = 9, adjusted-$P = 0.01$), but no differences between survival at the low and medium temperatures ($P = 0.09$) or between the medium and high temperatures ($P = 0.75$). Comparisons among temperatures within the variable regime indicated lower survival for the high temperature compared with the medium temperature ($t = 3.43$, df = 9, adjusted-$P = 0.02$), but no differences between the low temperature and either the medium temperature ($P = 0.11$) or the high temperature ($P = 0.15$).

Table 1. Estimated probability of *Lygus hesperus* egg survival under constant and variable temperatures.

Temp (°C)*	Regime (°C)	Probability of Survival to Hatch	
		Mean**	SE
15	Constant (±<0.5)	0.76 b B	0.08
	Variable (±8)	0.87 a AB	0.05
22	Constant (±<0.5)	0.88 a AB	0.05
	Variable (±8)	0.96 a A	0.02
29	Constant (±<0.5)	0.91 a A	0.04
	Variable (±8)	0.79 b B	0.08

* Mean daily temperature.
** Means corresponding to regime within a temperature followed by the same lowercase letter are not significantly different ($\alpha = 0.05$); means corresponding to temperatures within a regime followed by the same uppercase letter are not significantly different ($\alpha = 0.05$).

Diel periodicity of egg hatch. In the combined repetitions of the experiment, 725 eggs in total hatched during the nine observation periods that were analyzed under the medium temperature (mean = 22°C; constant $n = 332$, variable $n = 393$) and 785 eggs hatched during these periods under the high temperature (mean = 29°C; constant $n = 416$, variable $n = 369$). Contingency tables stratified by repetition of the experiment indicated differences between temperature regimes in the diel pattern of egg hatch for both medium ($Q_{GMH} = 148.0$, df = 8, $P < 0.01$; Fig. 3a) and high ($Q_{GMH} = 74.1$, df = 8, $P < 0.01$; Fig. 3b) temperatures. Under the medium temperature treatment, cell χ^2 values from the contingency table suggested hatch rate was disproportionately high under the constant temperature regime during the first two overnight periods (observed at 0700 h) compared with the variable regime (Fig. 3a). In contrast, hatch rate was higher under the variable regime at the second two observations at 1300 h compared with the constant regime. Diel patterns of hatch were roughly similar between constant and variable regimes under the high temperatures, except for the conspicuous absence of hatch between 1300 and 1900 h under the variable regime when temperatures were always >32°C.

Discussion

Hagstrum and Milliken (1991) cited reports for >70 insect species where developmental time under constant temperatures poorly represented developmental times under variable temperatures. In general, Hagstrum and Milliken (1991) found that, under variable temperatures, the higher temperatures of the range disproportionately influenced development compared with the lower temperatures. Our results for *L. hesperus* eggs were generally consistent with their report; observed developmental times for variable temperatures were greater than for constant temperatures when temperatures were relatively high, but development

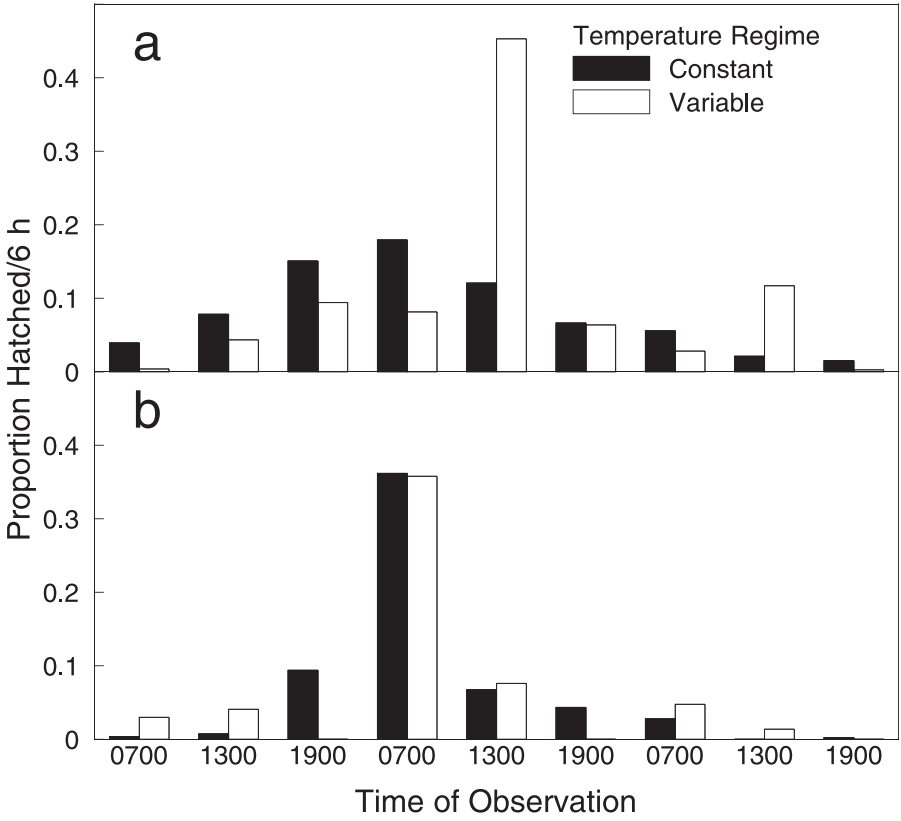

Fig. 3. Diel patterns of *Lygus hesperus* egg hatch under constant (±<0.5°C) and variable (±8°C) temperature regimes at (a) medium (mean = 22°C) and (b) high (mean = 29°C) temperatures.

was more rapid under low variable temperatures than under low constant temperatures (Fig. 1).

Hagstrum and Milliken (1991) cited results of Butler and Watson (1974) as an example where *L. hesperus* development differed under constant and variable temperatures. However, Butler and Watson (1974) reported the durations of *L. hesperus* developmental stages under variable temperatures were favorably indicated by estimates obtained under constant temperatures. In addition, their data exhibited considerable variation among instars and stages in the relationships between developmental times under respective constant and fluctuating temperatures. Their conclusion, that developmental times estimated under constant temperatures provide reasonable estimates of developmental times under fluctuating temperatures, likely resulted from at least two important limitations of their study. First, the experiment was conducted in an outside insectary and in field cages over alfalfa, neither of which allowed control of experimental temperatures. Second, the range of temperatures they observed within the cages was limited and

relatively low. With one exception, daily temperatures were between 17 and 30°C. This temperature range is similar to the medium variable temperature regime in our study that indicated little difference in development between constant and fluctuating temperatures. In contrast, our results indicate important influences of daily temperature fluctuations on developmental time.

The regression for egg developmental rates at constant temperatures suggested the relationship between temperature and developmental rate was approximately linear over the observed range of temperatures (Fig. 2), although Cooper and Spurgeon (2013) have shown the relationship is, in fact, nonlinear. In contrast, addition of a quadratic term to the regression equation was necessary to fit the data from the variable temperature regimes (Fig. 2). Hagstrum and Milliken (1991) reported that differences in developmental time between variable and constant temperatures increase with amplitude of the variable temperatures. Our temperature ranges were selected for ecological relevance based on reports of canopy temperatures in cotton. Those choices may have been fortuitous because use of more narrow temperature ranges may have obscured differences between constant and variable temperature regimes.

Extrapolation of both the simple and quadratic regressions predicted lower thermal thresholds for *L. hesperus* egg development slightly below 10°C (9.6 and 9.4°C, respectively). It is unlikely that these estimates are reasonable, because Cooper and Spurgeon (2013) demonstrated egg development to hatch at 10°C, although developmental time under those conditions was protracted ($>$70 d). It seems more likely that differences in egg developmental time between constant and variable temperatures would increase with decreasing temperatures until daily low temperatures are sufficiently low to induce acute or chronic chilling injury. The temperatures necessary to produce such injury have not been determined.

In addition to the influences of variable temperatures on egg developmental time, compared with constant temperatures, corresponding influences on egg survival were observed (Table 1). Variable temperatures apparently diminished thermal stress at low temperatures and induced thermal stress at high temperatures in comparison with the constant temperature regimes. However, under the high variable regime egg survival rates were higher than anticipated based on developmental abnormalities and incomplete development observed by Cooper and Spurgeon (2013) in response to temperatures similar to our daily highs. A longer sustained exposure to such temperatures is apparently necessary to cause irreversible injury to developing embryos. Whether nymphs respond similarly to high variable temperatures is not known, but experiments to obtain knowledge of survival rates under high-temperature conditions typical of plant water stress seem warranted.

Results under low temperatures have implications regarding overwintering mechanisms. Strong and Sheldahl (1970) reported that eggs laid before mid-February do not contribute to spring populations, based in part on the report of failure to hatch at low temperatures (Champlain and Butler 1967). However, egg (Cooper and Spurgeon 2013) and nymphal (Cooper and Spurgeon 2012b) development and survival, protracted adult reproductive development (Spurgeon and Cooper 2012), and extended host-free survival of adults (Cooper and Spurgeon 2015) have been demonstrated under low temperatures comparable to those observed by Champlain and Butler (1967). Cooper and Spurgeon (2015)

interpreted these combined results to suggest mechanisms other than adult diapause may contribute more to overwintering success than was previously recognized. The moderating influences of variable low temperatures on egg mortality we observed seem to support the likelihood of a substantial contribution of nondiapause strategies to overwintering success, especially in regions such as central Arizona where the adult diapause response is apparently incomplete (Spurgeon and Brent 2015).

Diel patterns of egg hatch at the medium temperature suggested hatch under the variable regime was accelerated during the warmest portion of the thermal cycle compared with the constant temperature regime (Fig. 3a). This effect was likely caused by a slowed hatch rate under the cooler nighttime temperatures and acceleration of hatch with increasing temperatures during the daytime. Under high temperatures, the most striking difference in patterns of egg hatch between constant and variable regimes was the absence of hatch during the warmest portion of the variable cycle. This effect may have been caused by simple inhibition of development or hatch by high temperatures, or it may represent a physiological or other mechanism to avoid hatch during unfavorably high temperatures. A similar modification of the periodicity of molting of *Spissistilus festinus* (Say) (Hemiptera: Membracidae) nymphs in soybean (*Glycine max* (L.) Merr.) in response to canopy temperatures was observed by Spurgeon and Mueller (1992).

Responses of *L. hesperus* populations to irrigation levels in cotton have been observed in the field (Asiimwe et al. 2014; Flint et al. 1994, 1996; Leigh et al. 1970; Munk and Goodell 2002). Results of these studies have not been wholly consistent, but they have often indicated increased *L. hesperus* population levels in heavily irrigated cotton. Of these studies, only Asiimwe et al. (2014) recorded cotton canopy temperatures, but the irrigation regimes studied did not induce differences in canopy temperatures among treatments. Therefore, it is not possible to discern the respective contributions of thermal conditions, differences in plant canopy size and structure, or preferences of the highly mobile adults where irrigation regime was observed to influence *L. hesperus* population levels. Increased knowledge of the ecology of *L. hesperus* and of its complement of natural enemies will provide baseline information necessary for applied studies of the mechanisms driving population responses in a changing thermal environment in cotton.

Acknowledgments

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